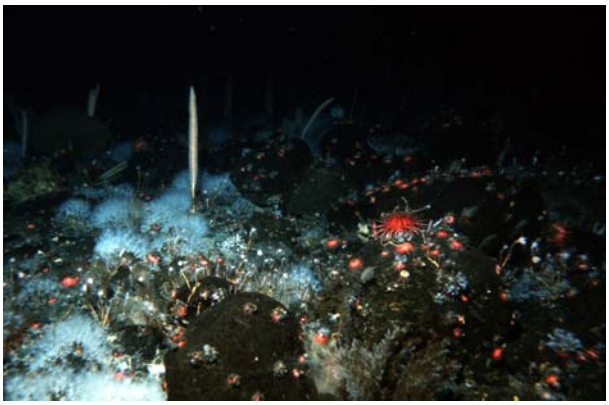

Shallow-water mega-epibenthic communities in the high Antarctic (Weddell Sea) and the west coast of the Antarctic Peninsula (Bellingshausen Sea)

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Universität Bremen, 2004

Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung in der Helmholtz-Gemeinschaft

Stiftung Alfred-Wegener-Institut
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„Gedruckt mit Unterstützung des Deutschen Akademischen Austauschdienstes und des Alfred-Wegener-Instituts für Polar und Meeresforschung“

To my parents and my brother,

for their unlimited love and support

"PRIMERO ESTABA EL MAR
TODO ESTABA OSCURO,
NO HABIA SOL NI LUNA,
NI GENTE, NI ANIMALES, NI PLANTAS
EL MAR ERA LA MADRE,
LA MADRE NO ERA GENTE
NI NADA, NI COSA ALGUNA.
ELLA ERA ESPIRITU DE LO QUE IBA A VENIR
Y ELLA ERA PENSAMIENTO Y MEMORIA"

Mitología Kogui
- Kogui: grupo indígena colombiano -

"FIRST THERE WAS THE SEA
EVERYTHING WAS DARK,
THERE WAS NEITHER SUN NOR MOON
NO PEOPLE, NEITHER ANIMALS NOR PLANTS
THE SEA WAS THE MOTHER,
THE MOTHER WAS NO PEOPLE
NOR ANYTHING, NOT EVEN SOMETHING.
SHE WAS THE SPIRIT OF WHAT WAS GOING TO COME
AND SHE WAS THOUGHT AND MEMORY"

Kogui Mythology
- Kogui: Colombian Indian group -

Contents

ABSTRACT

The topic of the present study is to compare shallow-water mega-epibenthic fauna of two biogeographic areas in the Antarctic, the Antarctic Peninsula (Bellingshausen Sea) and the high Antarctic (Weddell Sea). Continental shelves around Antarctica are unusual in being deep, and consequently shallow habitats at depths <150 m are scarce. In the Weddell Sea, for example, only two shallow sites with water depths between 55 and 160 m are known: the inner parts of Atka Bay and a recently discovered shallow bank off Four Seasons Inlet NE of Kapp Norvegia. In contrast, the Antarctic Peninsula has a true coast and thus, true littoral areas are common. This study (1) characterises and describes the distribution and spatial patterns of shallow-water (55-160 m) mega-epibenthic fauna in the Antarctic Peninsula (Marguerite Bay, Bellingshausen Sea) and at two sites in the high Antarctic (Weddell Sea), (2) analyses community structures and (3) compares benthic biodiversity in these areas at different spatial scales and with additional data from deep Antarctic shelf sites and corresponding shallow and deep areas in the Arctic, originated from previous studies.
In order to achieve the composition of the Antarctic benthic community, all organisms (>1 cm) were identified and counted on a total of 17 sea bed video transects conducted at 14 stations using a Remotely Operated Vehicle (ROV) during four Antarctic expeditions with R.V. *Polarstern* and R.R.S. *James Clark Ross* (ANT XIII, XV, XVII; JR37).

Multivariate analyses revealed significant faunal differences between Marguerite Bay (Bellingshausen Sea) and the Weddell Sea stations, Atka Bay and Four Seasons Bank. Echinoderms, especially ophiuroids, dominated Marguerite Bay, bryozoans and ascidians were abundant at Atka Bay, and hydroids and gorgonians were well represented at Four Seasons Bank. These differences can mainly be explained by the influence of local environmental conditions that are probably the primary factor shaping the Antarctic shallow-water epifauna, and not an intensive exchange with larger depths or limited dispersion due to scarce and isolated shallow areas. In addition, modes of reproduction and characteristics of the early life history (e.g. brooding, viviparity or budding) of key taxa may also shape patterns of species distribution in shallow benthic Antarctic communities.

Spatial patterns of Antarctic benthic shelf communities were analysed. Stations with non-significant "seriation" values, indicating no sharp faunistic discontinuities, have the smallest range of species or faunal-heterogeneity but intermediate values for species turnover along the videotransects. Conversely, stations with relatively good faunal seriation displayed broad ranges of species turnover. An analysis of depth zonation (60-143 m) at Four Seasons Bank (Weddell Sea) showed a clear gradient in faunistic assemblages. Different patterns are identifiable: a locally limited typical fauna, a patchwork of assemblages as well as continuous faunistic gradients. Combinations of these three scenarios can be considered as the rule in Antarctic mega-epibenthic communities.

The benthic fauna around Antarctica should not be viewed in isolation. Following this argument the faunistic and environmental parallelism with the Arctic in terms of biodiversity was studied. At a regional scale (γ-diversity), Antarctic sites (Bellingshausen and Weddell Seas) were richer in the number of mega-epibenthic taxa than the Arctic. In the Antarctic, all regional species numbers at shallow sites were higher than at deeper ones, but in contrast to the Arctic this could not be explained by a higher species turnover. No differences were found in species turnover (β-diversity) between the Arctic and Antarctic. At the local spatial scale (α-diversity), species numbers were higher in the Antarctic, what might be a reflection of a clearly higher regional diversity. In addition, different types of natural disturbances (e.g. predation pressure, iceberg scouring) might be other reasons for the higher local species numbers in the Antarctic.

ZUSAMMENFASSUNG

Gegenstand der vorliegenden Arbeit ist ein Vergleich der mega-epibenthische Flachwasserfauna zwischen zwei biogeographische Gebiete der Antarktis, der Antarktische Halbinsel (Bellingshausen Meer) und der Hochantarktis (Weddellmeer). Die Kontinentalschelfe um die Antarktis sind außergewöhnlich tief, daher sind flache Lebensräume mit Tiefen unter 150 m selten. Im Weddellmeer sind z.B. nur an zwei Stellen Wassertiefen zwischen 55 und 160 m bekannt: die südliche Atka Bay und eine kürzlich entdeckte flache Bank vor dem Four Seasons Inlet nordöstlich von Kapp Norvegia. An der Antarktischen Halbinsel (Bellingshausen Meer) hingegen gibt es eine echte Küste, und deswegen sind Flachwassergebiete häufig. Im Rahmen dieser Arbeit habe ich (1) die Verteilung und räumlichen Muster der mega-epibenthischen Flachwasserfauna der Hochantarktis (Weddellmeer) und der Antarktischen Halbinsel (Marguerite Bay, Bellingshausen Meer) in 55 bis 160 m Tiefe beschrieben und charakterisiert, (2) deren Lebensgemeinschaften analysiert und (3) die benthische Biodiversität dieser Gebiete auf verschiedenen räumlichen Skalen miteinander vergleichend analysiert und mit zusätzlichem Datenmaterial aus tiefen antarktischen Schelfgewässern und entsprechenden Flach- und Tiefwassergebieten der Arktis verglichen.

Um die Zusammensetzung der antarktischen Benthosgemeinschaften zu erfassen, habe ich auf insgesamt 17 Videotransekten auf 15 Stationen alle erkennbaren (>1 cm) Organismen bestimmt und gezählt. Dieses Videomaterial wurde mit einem ferngesteuerten Unterwasserfahrzeug (ROV) während vier Antarktis-Expeditionen mit „*Polarstern*“ und „*James Clark Ross*“ (ANT XIII, XV, XVII; JR37) aufgenommen.

Multivariate Analysen zeigen, dass sich die Fauna in den Untersuchungsgebieten im Bellingshausenmeer (Marguerite Bay) und im Weddellmeer (Atka Bay und Four Seasons Bank) deutlich unterscheiden Echinodermen, besonders Ophiuroiden, dominierten in der Marguerite Bay, während Bryozoen und Ascidien in der Atka Bay die höchsten Abundanzen aufwiesen Auf der Four Seasons Bank waren Hydroiden und Gorgonarien besonders zahlreich. Diese Unterschiede können vor allem durch den Einfluß der lokalen Umweltbedingungen erklärt werden, die vermutlich die

antarktische Flachwasser-Epifauna grundsätzlich prägen, und nicht ein intensiver Austausch mit größeren Tiefen oder eingeschränke Ausbreitung wegen der wenigen isolierten Flachwassergebiete Zudem können auch der Reproduktionsmodus und Eigenschaften der Jugendstatien von Schlüsselarten (z. B. brütend, Lebendgebärend oder Knospend) die Verteilungsmuster der Arten in flachen benthischen Gemeinschaften in der Antarktis beeinflussen.

Räumliche Muster von antarktischen benthischen Schelfgemeinschaften wurden analysiert. In der mega-epibenthischen Flachwasserfauna gefundene Muster für "reihenweise Anordnung" ["seriation"] (Zonierung ohne scharfe Unterbrechung) und Tiefenzonierung wurden durch Beispiele hervorgehoben. Stationen mit nicht signifikanten Werten für eine reihenweisen Anordnung (seriation), also ohne scharfe Unterbrechung in der Fauna hatten die geringsten Artenzahlen bzw. geringste faunistischer Heterogenität, aber mittlere Werte für den Faunenwechsel (species turnover) entlang der Videotransekte. Im Gegensatz dazu zeigten Stationen mit relativ guter reihenweiser Anordnung einen erheblichen Faunenwechsel. Eine Analyse der benthische Tiefenzonierung (60-143 m) der Four Seasons Bank (Weddellmeer) zeigt einen klaren Gradienten der Artenassoziationen zu geben. Verschiedene Muster konnten identifiziert werden: eine lokal begrenzte typische Fauna, ein Nebeneinander von Assemblages und kontinuierliche faunistische Gradienten. Kombinationen dieser drei Möglichkeiten können in antarktischen mega-epibenthischen Gemeinschaften als die Regel betrachtet werden.

Die benthische Fauna um den Antarktischen Kontinent sollte nie isoliert betrachtet werden. Diesem Argument folgend, ist es ein wurde versucht Parallelen zur Arktis vor Nordostgrönland zu finden. Auf der regionalen Skala (γ-Diversität) wiesen die antarktische Gebiete (Bellingshausen und Weddellmeer) eine größere Anzahl mega-epibenthischer Arten auf als die Arktis. In der Antarktis waren alle regionalen Artenzahlen in flachen Gebiete höher als in tieferen, aber im Gegensatz zur Arktis konnte dies nicht durch einen höheren Faunenwechsel erklärt werden. Es gab keine Unterschiede der Zu- und Abwanderung von Arten (β-Diversität) zwischen der Arktis und der Antarktis. Auf der lokalen Skala (α-Diversität) waren die Artenzahlen in der Antarktis höher, was möglicherweise eine höhere

regionale Diversität widerspiegelt. Zudem können verschiedene natürliche Störungen (z. B. Fraßdruck, Eisbergkratzer) ein weiterer Grund für die höheren lokalen Artenzahlen in der Antarktis sein.

RESUMEN

El tema central de este estudio es comparar la fauna megaepibentónica de aguas someras de dos áreas biogeográficas en la Antártida, la Peninsula antártica (Mar de Bellinghausen) y la Antártida alta (Mar de Weddell). La plataforma continental que circunda la Antártida es excepcionalmente profunda, y por consiguiente los habitats someros con profundidades <150 m son escasos. En el Mar de Weddell, por ejemplo, solo dos lugares con profundidades entre 55 y 160 m son conocidos: las partes internas de la Bahía Atka y el banco somero "Four Seasons" ubicado al nororiente del cabo "Norvegia" descubierto recientemente . Contrario a ésto, la península antártica tiene una costa verdadera y por lo tanto, las áreas litorales son comunes. Este estudio (1) caracteriza y describe la distribución y los patrones espaciales de la fauna megaepibentónica de aguas someras (55-160 m) en la península antártica (Bahía Marguerite, Mar de Bellinghausen) y en dos sitios en la Antártida alta (Mar de Weddell), (2) analiza la estructura de la comunidad y (3) compara la biodiversidad béntonica en estas áreas a diferentes escalas espaciales, y compara éstos datos a su vez, con datos adicionales de áreas profundas de la plataforma continental antártica y áreas someras y profundas del Artico, originados en estudios anteriores. Con el objetivo de obtener la composición de la comunidad bentónica de la Antártida, se identifico y contó todos los organismos (>1 cm) en un total de 17 video transectos del fondo marino realizados en 14 estaciones, empleando un vehículo operado a control remoto (ROV) durante cuatro expediciones antárticas con las motonaves de investigación científica *Polarstern* y R.R.S. *James Clark Ross* (ANT XIII, XV, XVII, JR37)

Los análisis multivariados mostraron diferencias faunísticas significativas entre la Bahía "Marguerite" (Mar de Bellingshausen) y las estaciones del Mar de Weddell, Bahía Atka y el banco "Four Seasons". Los equinodermos, especialmente ofiúridos, dominaron Bahía "Marguerite", bryozoos y ascidias fueron abundantes en la Bahía Atka, e hidroídeos y gorgonias estuvieron bien representados en el banco "Four Seasons". Estas diferencias pueden ser básicamente explicadas por la influencia de las condiciones ambientales locales que son probablemente el príncipal factor que moldea la epifauna antártica de aguas someras y no por un intercambio intensivo con profundidades mayores, o por una

dispersión limitada debido a la escasez y el aislamiento de áreas someras. Adicionalmente formas de reproducción (e.g. incubación, viviparísmo o gemación) y características de la historia temprana de vida de las taxas clave, también pueden moldear patrones de distribución de especies en las comunidades bentónicas someras de la Antártida.

Patrones espaciales de las comunidades antárticas bentónicas fueron analizados. Estaciones con valores no significativos de "seriación", indicando discontinuidades faunísticas no fuertemente marcadas, presentan el rango mas bajo de especies o heterogeneidad faunística pero valores intermedios para rotación de especies (species turnover) a lo largo del video transecto. Contrariamente estaciones con una "seriación" faunística relativamente buena desplegaron rangos amplios de rotación de especies. Un análisis de zonación por profundidad (60-143 m) mostro en el banco "Four Seasons" (Mar de Weddell) un gradiente claro de asociaciones faunísticas. Diferentes patrones son identificables: una fauna típica localmente limitada, un mosaico de asociaciones, al igual que gradientes faunísticos continuos. Combinaciones de éstos tres escenarios pueden ser consideradas como la norma en las comunidades megaepibentónicas antárticas.

La fauna bentónica que circunda la Antártida no debe ser vista aisladamente. Siguiendo etse argumento, el paralelismo faunístico y ambiental con el Artico en términos de biodiversidad fue estudiado. A una escala regional (diversidad γ) las áreas antárticas estudiadas (Mar de Bellingshausen y Mar de Weddell) fueron mas ricas en el número de taxa megaepibentónica que en el Artico. En las áreas someras de la Antártida, todos los números de especies regionales fueron mayores que en áreas profundas, pero en contraste con el Artico esto no puede ser explicado por una rotación de especies mas alta. No hubo diferencias considerando las comparaciones entre rotación de especies (diversidad β) en el Artico y la Antártida. A una escala espacial local (diversidad α) el número de especies fue mas alto en la Antártida, lo cual puede ser el reflejo de una clara diversidad regional alta. Adicionalmente, diferentes tipos de perturbaciones naturales (e.g. presión por predación, o perturbaciones por témpanos de hielo) pueden ser otra razón del alto número de especies locales en la Antártida.

1 Introduction

1.1 Origin of the Antarctic fauna

The origin of the Antarctic marine fauna has attracted the curiosity of researchers since it is unique, it shows only few similarities with that of adjacent continents and some elements appear to represent an ancient relict fauna. As a consequence, several hypotheses have been suggested in order to describe the origin and evolution of the Antarctic fauna (Knox and Lowry 1977, Lipps and Hickman 1982, Dayton 1990). (1) Time stability hypothesis: *The Antarctic fauna has undergone extensive evolution "in situ"*, since the Cretaceous or even earlier, before Gondwana broke up (Dell 1972, Clarke and Crame 1989). (2) Stepping stones hypothesis: c*ool-temperate species dispersing from South America via the Scotia Arc*. Different elements of exchange had been shown between the fauna of the Antarctic Peninsula and South America (Watling and Thurston 1989, Clarke and Johnston 2003). This immigration process could apparently be achieved by using these islands as stepping stones. (3) Colonization hypothesis: e*urybathic and psychrospheric fauna derived from adjacent deep-water basins*, immigration being facilitated by similar conditions in the environment. However, the latter hypothesis has been particularly controversial taking in account the opposite process (Sieg 1988). Eurybathy in Antarctic benthic invertebrates is assumed to have been controlled by glacial-interglacial cycles. Species without the ability of moving into the deeper waters of the continental slope during glacial periods were likely to become extinct (Galéron et al. 1992, Brey et al. 1996).

A certain level of consensus have been achieved by biogeographers in that most of the Antarctic benthos is old and represents original propagules that moved southwards with the continent (Picken 1985). Although considerable amount of information is available process

and mechanisms (e.g. dispersal, vicariance or competence) undergone in order to generate the modern fauna are not well known (Orensanz 1990). Within this context, Clarke and Crame (1989, 1992) suggested that the polyphyletic feature of this fauna, does not allow to make reference to a single origin for the overall fauna. For example teleost fishes (notothenioids), amphipods, isopods, pycnogonids have undergone marked radiation in the Southern Ocean (Clarke and Johnston 2003) whereas, e.g polychaetes could have just disperse and colonize, or just been part of the ancient fauna (Knox 1977). Different origins have to been taken in account, and, it also depends on which taxonomic group or level is of interest.

1.2 Biogeographic remarks: Antarctic Peninsula and high Antarctic

The faunas of the Antarctic Peninsula and the high Antarctic Weddell Sea have long been considered to belong to different zoogeographical regions (Hedgpeth 1971). These two areas are distant from each other by about 2000 km, and are characterised by a strong seasonality with changing light regime, ice coverage (Gutt 2000), primary production, sedimentation (Arntz et al. 1992), but relatively constant physical conditions (Klages 1993; Klages et al. 1995). However, these two regions differ in one striking aspect that is relevant to the benthos: the Antarctic Peninsula has a true coast and thus, true littoral areas are common whereas in the Weddell Sea almost all shallow waters are covered by the floating margins of the continental ice caps.

The continental shelves around Antarctica are unusual in being deep, commonly as much as 800 m in some areas (Clarke 1996b). More than 95% of the coastline and near shore region of the high Antarctic is covered by floating or grounded ice, thus deep waters (>150 m) predominate and shallow areas are scarce (Drewry 1983; Gutt 2000). In the Weddell Sea only

two shallow sites with water depths between 55 and 160 m are known: the inner parts of Atka Bay and a recently discovered shallow bank off Four Seasons Inlet NE of Kapp Norvegia. This bank seems to host a faunal assemblage which differs from that of well investigated adjacent deeper waters.

The benthos of the Southern Ocean is influenced by a number of factors including depth, sediments, bottom topography, habitat, oceanography, ice scouring, competition and predation (Dayton et al. 1970, 1974, Gallardo 1987, Arntz et al. 1994, Clarke 1996a, 1996c, Slatery and Bockus 1997, Stanwell-Smith and Barnes 1997, Gutt 2000). Furthermore, Antarctic epifaunal assemblages have been described basically as circumpolar by many authors (Hedgpeth 1971, Knox and Lowry 1977, Richardson and Hedgpeth 1977, Voß 1988), due to the similarity of conditions in the sea around the continent and the circum-Antarctic current systems. The existence of comparable assemblages has been doubted by others including White (1984), Picken (1984) and Gallardo (1987), and recent evidence indicates the existence of quite a number of genetically different species of very similar morphological appearance (e.g. Held 2003 for isopods). It has been defined the circum-Antarctic occurrence of many species plus smaller provinces or regions may be the dominant distribution pattern (Dayton 1990).

1.3 Imaging techniques

Research on patterns and processes in benthic communities of the Southern Ocean are of general interest to characterize their structure, to describe their function and to understand their development (White 1984, Arntz et al. 1994, Clarke 1996c).

In general, distributional studies of Antarctic macrobenthos have relied on traditional sampling techniques (e.g. bottom trawls, dredges, grabs) (Knox 1960, Hedgpeth 1969, Dell 1972, Arnaud 1977, Sarà et al. 1992) which are basically destructive. Trawls and dredges in particular suffer from the disadvantages of destroying any structure in the community (e.g. ecological associations), damaging many specimens and mixing samples from different assemblages (Clarke 1996c), and should therefore be restricted to occasions when large amounts of material are required.

Imaging technique is one major modern survey method (Pilgrim et al. 2000) which provides information to apply new analytical methodologies e.g. landscape approach (Garrabou et al. 2002) that allow to obtain new quantitative results and scientific insights in ecological research. The use of imaging techniques allows to observe non-destroyed benthic assemblages with a high resolution over large areas. These techniques have been implemented in tropical (Hughes and Jackson 1985, Edmunds and Wittman 1991), temperate (Schneider et al. 1987, Parry et al. 2003) and high latitudes (Gutt and Starmans 1998, Teixidó 2003). As a consequence, a variety of marine communities have been investigated, e.g coral reefs (Done 1981, Carleton and Done 1995, Aronson and Swanson 1997, Ninio et al., 2003), rocky (Garrabou et al. 2002) and deep-sea (Grassle et al. 1975, Kaufmann et al. 1989, Hovland et al. 2002). Furthermore such modern techniques have been implemented as useful tools in monitoring programmes for conservation policies (Cooper et al. 1987, Aronson et al. 1994, Vago et al. 1994, Connell et al. 1997, Edmunds 2002).

In the Antarctic Bullivant (1959, 1961) was pioneer in the use of imaging methods as a sampling method for benthic communities. However, such studies were then largely ignored and were not used for quantitative analyses (Clarke 1996c). Recently, the use of modern

imaging techniques have been implemented in the Antarctic, and ROVs have provided powerful new insights on the ecology of the benthos of the Southern Ocean.

ROV deployments have been planned and carried out in such a way, that the scientific information retained on the images could be transformed to quantitative ecological data. In this study a ROV was employed as a sampling method, which is highly effective for marine ecological studies at large spatial scale for work with the mega-epibenthos, due to its high spatial resolution (Clarke 1996a), since abundances can be determined separately for each square metre. Recent advances in Remotely Operated Vehicle (ROV) technology allow the recording of a continuous stream of images with sufficient resolution and colour saturation to identify the fauna and determine fine-scale substrate characteristics (Malatesta et al. 1992).

Although these methods cannot fully replace traditional sampling, e.g. for small fauna or infauna in general, they are contributing increasingly to biodiversity assessments. Continuous video-records have made possible scientific research on iceberg scouring and succession on megabenthic assemblages and allowed the verification of ecological hypotheses (Gutt et al. 1996, Gutt 2001, Gutt and Starmans 2001, Starmans et al. 1999, Starmans and Gutt 2002). Furthermore, such video records enable analyses at different scales (ca. 1 to 1000 m) within a single transect e.g relations of demersal fish with specific habitats (Gutt and Ekau 1996) or patchiness of sessile fauna (Gutt and Starmans 2003, Gutt and Piepenburg 2003). In addition, detailed information on spatial community structure and specific architectonic arrangements of the mega-epibenthos: “three-dimensional assemblages”, were possible to observe and quantify (Barthel and Gutt 1992, Gutt and Schickan 1998, Gutt and Starmans 1998).

1.4 Objectives of this study

This study was designed to answer the following scientific questions:

1. Are there differences in zoogeographic patterns at the community level in the shallow-water benthic fauna between the high Antarctic (Weddell Sea) and the Antarctic Peninsula region (Bellingshausen Sea)?

2. Are Antarctic shallow-water mega-epibenthic communities shaped by circumpolar dispersion or local conditions?

3. What is the structure of Antarctic mega-epibenthic communities at intermediate scales?

4. Is the mega-epibenthos inhabiting the Antarctic shelf in the Weddell and Bellingshausen seas really more diverse than that of the Arctic?

5. Does shallow-water polar mega-epibenthos exhibit a higher heterogeneity than the benthos on the deeper shelves?

2 Study areas

The investigations presented here were carried out in the Weddell and Bellingshausen seas in the Southern Ocean, complementary material was used from one additional investigation area off north-east Greenland and deep areas in the Antarctic.

2.1 Weddell Sea

The area of the Weddell Sea is approx. 2.3 million km^2 and forms the southernmost part of the Atlantic Ocean (Carmack and Foster 1977, Stewart 1990) (Fig. 1). The continental shelf reaches depths of down to 500 m (Carmack and Foster 1977, Elverhφi and Roaldset 1983). The sites selected for this study comprised the narrow shelf of the eastern Weddell Sea, including basically the areas of Kapp Norvegia and Atka Bay. Seasonal ice covers the continental shelf and extends beyond the continental break (Tréguer and Jacques 1992) but a coastal polynya of interannual variation in size may occur, that due to katabatic winds may remain also open in winter (Hempel 1985, Hellmer and Bersch 1985). Water temperature close to the seafloor varies from –1.3 °C to –2.0 °C (Fahrbach et al. 1992). The oceanographic circulation of the Weddell Sea is characterised by the Weddell gyre. Current directions vary strongly during the year in the Kapp Norvegia area, between 197˚ and 257˚ at different locations and depths (Fahrbach et al 1992). Primary production is characterised by a marked summertime peak (Gleitz et al. 1994, Park et al. 1999), reflected by the organic matter flux from surface waters to the seabed (Bathmann et al. 1991, Gleitz et al. 1994). A general feature of the eastern part of the Weddell Sea is the biogenic sediment (Grobe 1986).

In some places sponge spicule mats and fragments of bryozoans are important components forming biogenic sediment beds. An overview of the distribution of the different sediment types is given by Voß (1988).

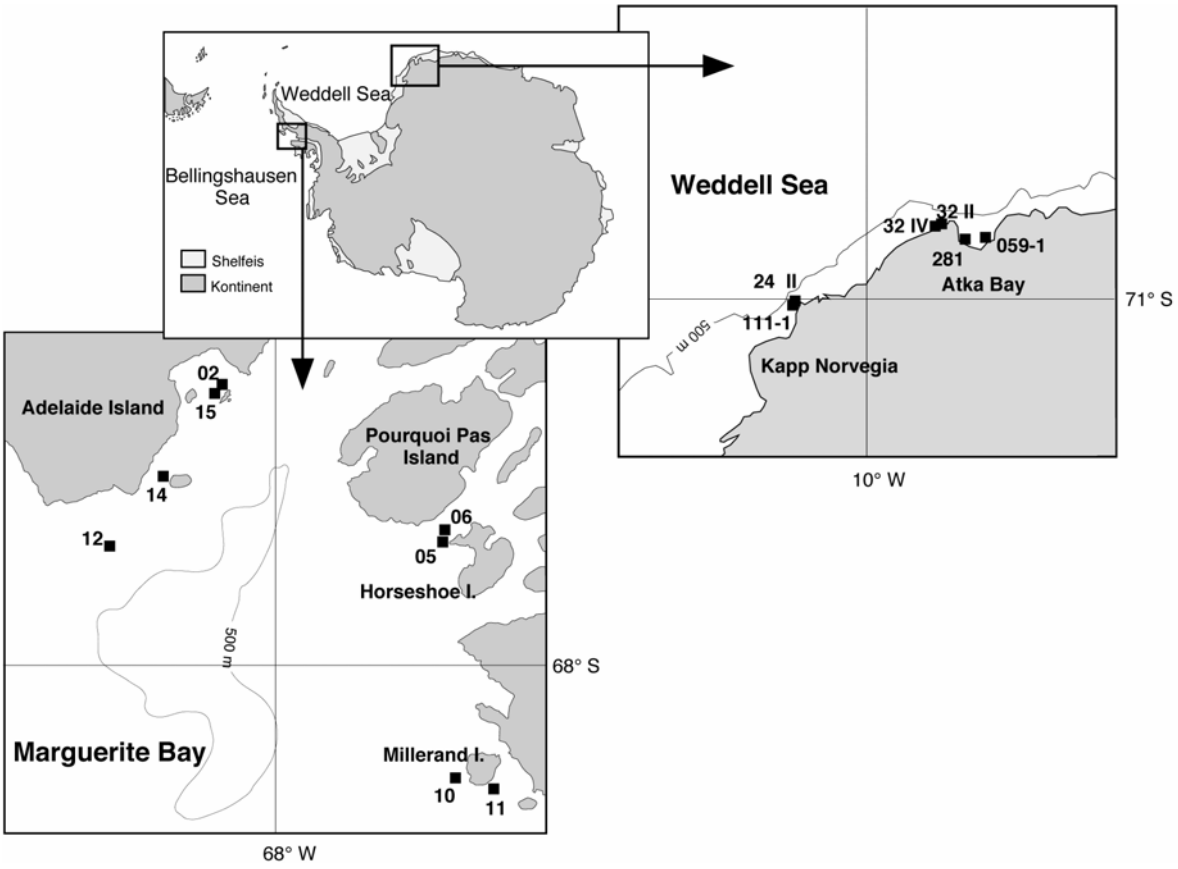
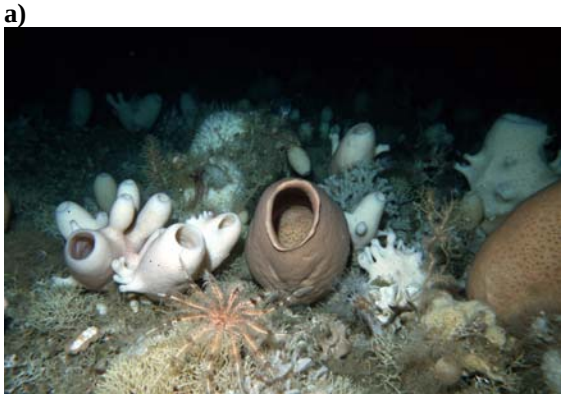


Fig. 1 Areas of investigation: Bellingshausen Sea (Marguerite Bay) and Weddell Sea (Atka Bay, Kapp Norvegia), Antarctica

Due to the submerged continental shelf and the glaciated coast shallow-water areas (<150 m) in the Antarctic are scarce. In the eastern Weddell Sea two such sites are known, one in and west of Atka Bay and the other being a shallow bank off Four Seasons Inlet (11°28'W, 71°07.5'S) NE of Kapp Norvegia (Fig. 1).

2.1.1 The benthic fauna of the eastern Weddell Sea

a)



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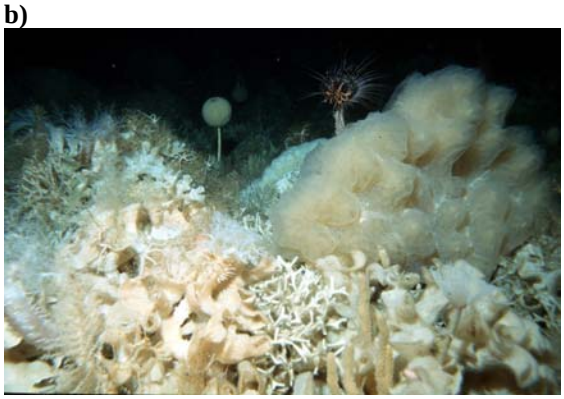

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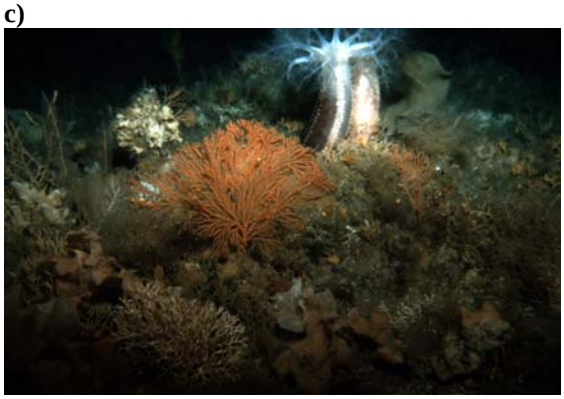

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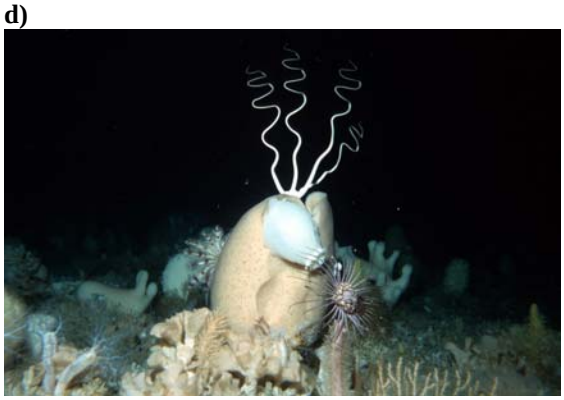

The benthic fauna in the eastern Weddell Sea around Kapp Norvegia and Atka Bay is dominated by a great number of sessile suspension feeders such as sponges, gorgonians ascidians and bryozoans, which at some localities cover the sediment completely (Gutt and Starmans 1998, Starmans et al. 1999). In this area assemblages are characterised by complex three-dimensional structures, the so-called "multistoried assemblages" (Fig.2) (Knox and Lowry 1977, Dearborn et al. 1986). Especially hexactinellid sponges, gorgonians and bryozoans play an important role providing biogenic substrata for a significant number of Antarctic invertebrates. The benthos in this area is characterised with intermediate to high diversity, high values of biomass and a patchy distribution of organisms (Gutt and Starmans 1998, Gili et al. 2000).

Fig. 2 Eastern Weddell Sea fauna. **a)** Crinoids, bryozoans and hexactinellid sponges, (125 m). **b)** bryozoans, *Aplidium* sp. (Ascidiacea) *Corymorpha parvula* (Hydrozoa) and *Stylocordyla borealis*, round (Demospongiae), (102 m). **c)** *Ekmocucumis turqueti* (Holothuroidea), gorgonians and bryozoans, (64 m). **d)** *Front* bryozoans and *Corymorpha parvula* (Hydrozoa). *Middle* hexactinellid sponge with *Psolus* spp. (Holothuroidea) and *Astrotoma agassizii* (Ophiuroidea), (119 m).

Most of the coastal areas on the Weddell Sea shelf display differences in community composition on small spatial scales, generally in response to differences in substrata, topography or hydrography (Gutt 2000). Voß (1988) characterised the sediments of the eastern Weddell Sea by the presence of sandy bottoms, bryozoan debris, sponge spicule mats and a few stones. A first description of the benthic assemblages in this area was made by Voß (1988) and it was then modified by Gutt and Starmans (1998). They distinguished three basic communities on the shelf of the eastern Weddell Sea: "Eastern", "Southern" and "Trench", with the "Eastern community" as the richest of the three.

2.2 Bellingshausen Sea

The Bellingshausen Sea is located in the Pacific sector of the Southern Ocean, between Thurston Island in the west and the Antarctic Peninsula in the east (Stonehouse 2002) (Fig. 1). The continental shelf is very extensive (150-400 km) and in its narrow parts, very similar to the southeastern Weddell Sea. Water temperatures range from –1.8 °C to +0.3 °C (Stambler 2003). Two water masses characterise the area in the Bellingshausen Sea (Hellmer and Bersch 1985). Biogenic sediments are not common in Marguerite Bay (Brockington et al. 2001). Soft bottoms with different proportions of gravel, sand and films of diatoms are characteristic of this area (Bryan 1992).

Shallow-water stations (<150 m) in the Bellingshausen Sea were located in northern Marguerite Bay (at Adelaide Island), where a true coast and adjacent shallow waters are found, in contrast to the eastern Weddell Sea (Kennedy and Anderson 1989, Bonn et al. 1996). The land as well as the seascape, and consequently the coastline, are here quite variable and heterogeneously structured.

2.2.1 The benthic fauna of the Bellingshausen Sea

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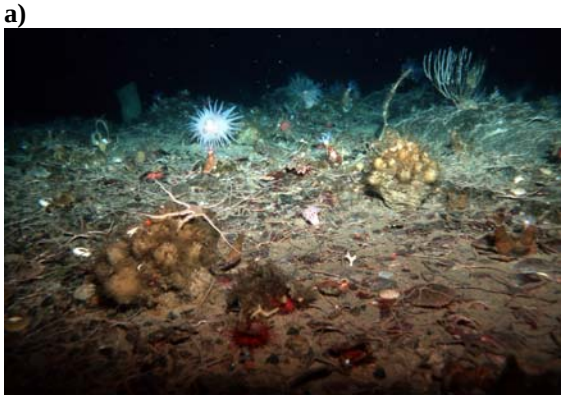

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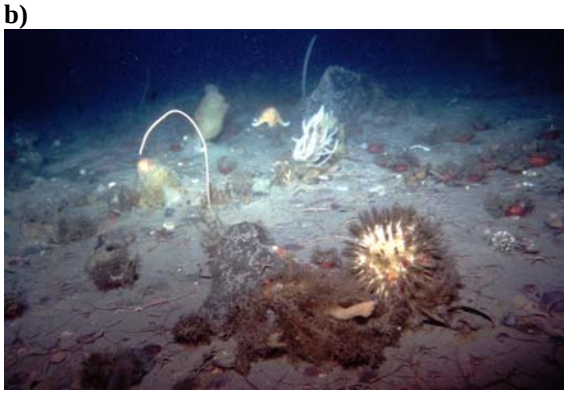

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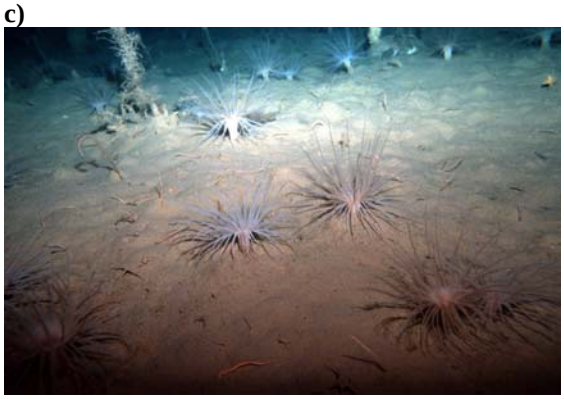

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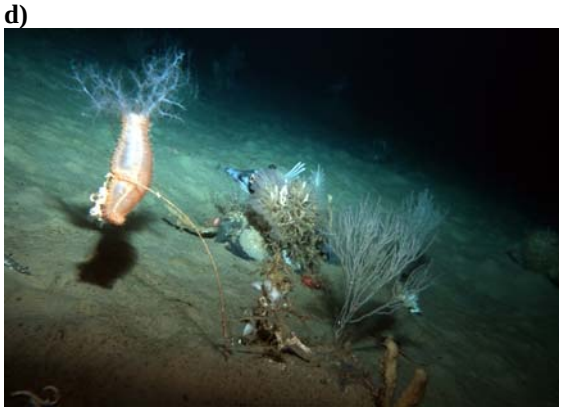


In contrast to the Weddell Sea, the mega-epibenthos in the Bellingshausen Sea has not been intensively studied. However, several studies on the benthos at depths between 0-45 m have been a subject of particular interest north of the Antarctic Peninsula (Zamorano 1983, Wägele and Brito 1990, Rauschert 1991, Nonato et al. 2000, Barnes and Arnold 2001, Barnes and Brockington 2003) but research on deeper areas has been scarce.

The benthic fauna of the Antarctic Peninsula is represented mainly by a true soft-bottom community dominated by polychaetes, molluscs and bivalves (Gallardo et al. 1977, Mühlenhard-Siegel 1988, Saiz-Salinas et al. 1998). Further south, Starmans et al. (1999) studied the mega-epifauna and noted that assemblages of suspension feeders dominated by sponges and bryozoans are almost

Fig. 3 Bellingshausen Sea fauna. **a)** *Rosella racovitzae* (budding type) (hexactinellid), ophiuroids, shells of *Adamussium colbecki* (Bivalvia), (76 m). **b)** *Cinachyra antartica* (Demospongiae) , *Primnoella* spp.(Gorgonacea), *Sterechinus neumayeri* (Echinoidea), (70 m). Soft sediments: **c)** Ceriantharia spp. (170 m), **d)** Holothuroidea and *Trematomus* spp. (Pisces), (157 m).

absent in this region. In addition, these assemblages lacked the pronounced three-dimensional architecture reported for communities in the Weddell Sea (Fig. 3). The authors noted the presence of sandy bottoms and the relative abundance of drop stones. They also remarked high abundances of sessile anthozoans, mobile echinoderms, and bryozoans.

2.3 North-east Greenland

The Arctic investigation site was the high-Arctic shelf region off northeast Greenland in the Greenland Sea (Fig. 4). At this site the bathymetry is complex and the shelf consists of a system of shallow banks (< 100 m) separated by troughs and trenches with depths > 400 m. Fine-grained sediments cover the sea floor, particularly in the shelf troughs and at the slope, whereas coarser fractions predominate on the shallower banks (Piepenburg 1988). Here a pronounced depth zonation is a principal feature of the megabenthic distribution (Piepenburg and Schmid 1996).

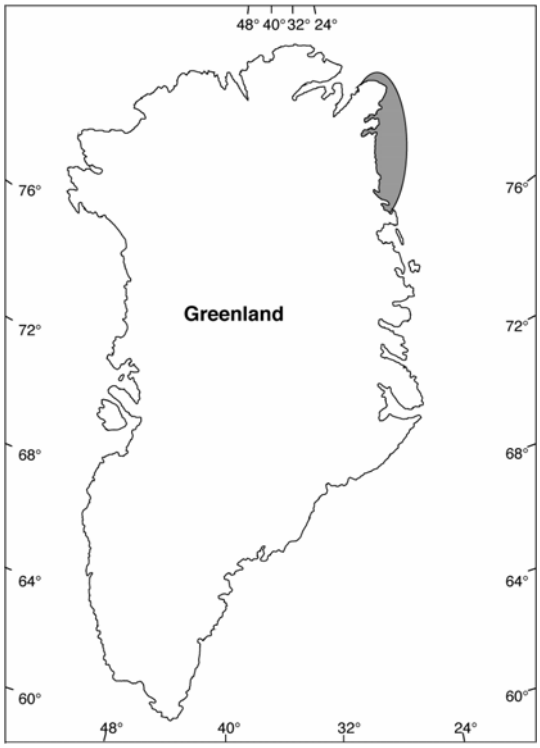


Fig. 4 Area of investigation: off Northeast Greenland, Greenland Sea

3 Material and Methods

3.1 Video sampling

Sea-bed video observing transects were conducted using a ROV ("Sprint 101") (Fig. 5) at shallow depths between 55-160 m (Fig. 1 and 4). With the exception of station ANT XIII, 24II (see below), each single station is comprised of a video transect lasting approximately 60 minutes. The length of the transects was determined by the drift of the ship and the width (ca. 0.5 m) by two parallel laser beams, which acted as a scale on the image.

Fig. 5 Remotely Operated Vehicle (ROV), "Sprint 101"

In the Weddell Sea, video records were taken during the expeditions ANT XIII/3, ANT XV/3 and ANT XVII/3 of the German R/V "Polarstern" (for details on the expeditions see Arntz and Gutt 1997, 1999; Arntz and Brey 2001). The study site west of Atka Bay is a bank being unusually shallow at the ice-shelf cost. Another site in the Atka Bay rises continuously at a width of approximately 5 km to the ice-shelf coast, where at a water depth of 55 m the ice is locally in contact with the seafloor (Grosfeld et al. 1989). The

shallow bank off Four Seasons Inlet (11°28'W 71°07,5'S) NE of Kapp Norvegia is approximately 1.7 km long in its north-west south-east extension and on average 320 m wide; it rises from a plateau at 170 m depth to 60 m depth at its shallowest part. Its north-eastern slope is relatively steep over the complete depth ranging from approximately 150 to almost 60 m. At Kapp Norvegia the complete ROV station (ANT XIII, stn 24II) was split into four different transects: at the north-eastern side it was separated according to depth from the deep to the shallow into three distinct transects; after a certain distance without video observation the fourth part of this transect (ANT XIII, stn 24II) is situated at the south-western slope of the bank at around 120 m depth. One additional transect has been videotaped at this slope between 60 and 90 m (ANT XVII, Stn 111-1).

In northern Marguerite Bay (Bellingshausen Sea) off the west coast of the Antarctic Peninsula (Fig. 1), video transects were undertaken from the British Antarctic Survey research vessel R.R.S. “James Clark Ross” (cruise JR37). The transects covered depths below 57 m.

For data used in the third publication the sampling method was the same but deeper stations in the Antarctic were video-taped during the expeditions ANT VI/3 (eastern Weddell Sea) and ANT XI/3 (Bellingshausen Sea) (Fütterer 1988, Miller and Grobe 1996). Arctic samples for deep and shallow water depths were taken off Northeast Greenland (Greenland Sea) during ARK IX/2-3 (Hirche and Kattner 1994) (Fig. 4). These data were available as raw material and were recalculated for the analyses in order to provide an optimum in compatibility e.g. in terms of sample size.

Due to logistics and temporal constraints, measurements of ecologically relevant environmental parameters being directly linked to my benthological concept were not possible, especially since this approach combines results from four expeditions and three investigation areas.

3.2 Identification

All organisms > 1 cm were counted and identified to the lowest possible taxonomic level at the given optical resolution of the cameras. Organisms were identified based on literature (Thomson and Murray 1880 to 1889, Discovery Committee Colonial Office 1929 to 1980, Sieg and Wägele 1990) and experts, who identified true material from the study sites and also assisted in the identification of different taxa. Most of these specialists contributed to a comprehensive species list for the Weddell Sea (Gutt et al. 2000). Colonies of colonial taxa were counted and treated as single individuals in the statistical analyses. Where this approach proved impossible because of the irregular shape of the colony, percentage cover of the sea floor was determined and used as a proxy for true abundances. In order to achieve a better identification of the organisms, an average of 100 still photographs for each station were also made by the ROV on the same transects and consulted in addition to the video observations.

3.3 Data analyses

Detailed descriptions of the methods applied are included in the publications attached. Here I give a general overview of the data analysis used in this study.

Multivariate methods available in the statistical analysis package PRIMERv5 (Clarke and Gorley 2001) were applied to a matrix containing abundances for each station (Publication I) or subsamples (Publication II). Similarities between stations (or subsamples) and taxa were calculated using the Bray-Curtis coefficient (Clarke and Warwick 1994). Non-metric multi-dimensional scaling (MDS) was employed for ordination (Kruskal and Wish 1978). Significance tests for differences among sites were carried out using one-way ANOSIM (Clarke and Green, 1988) permutation tests (Publication I). The nature of the community

groupings resulting from the MDS ordination was explored further by using the similarity percentages (SIMPER) routine to determine the contribution of individual taxa to the average dissimilarity between samples (Clarke 1993) (Publication I).

For horizontal seriation (Clarke et al. 1993) and depth zonation the following procedures were used (Publication II):

Horizontal seriation: Firstly non metric multidimensional scaling (MDS, Kruskal and Wish 1978) was performed. Secondly, the degree of seriation was visualized by joining the points in the MDS, in the order of the subsamples along the transect (Clarke et al. 1993). After these analyses an index of multivariate seriation (IMS) (Clarke et al. 1993) was calculated to determine the extent to which the community changes in a smooth and regular fashion along each transect. In order to achieve a measure of species turnover, Bray- Curtis similarity between all pairwise permutations of subsamples was used (Magurran 1988).

Depth zonation: Firstly multivariate analyses were performed as mentioned above. In addition inverse analysis (Field et al. 1982) was performed in order to cluster species that tend to co-occur in similar ratios across the subsamples. Finally univariate measures of diversity and evenness were computed: total number of taxa (S), Pielou's evenness ($J' = H'/ \log_e S$) and Hill's numbers diversity ($N1 = \exp(H')$) with $H' = -\Sigma_i p_i \ln(p_i)$ and p_i= relative abundance per station of species i (Clarke and Warwick 1994).

Different measures of biodiversity were performed at different spatial scales in mega-epibenthic communities in the Antarctic and the Arctic (Publication III). Data were analysed according to univariate and multivariate measures in the following way:

Within-habitat (α) diversity: Firstly univariate measures of diversity and evenness were computed for each group of stations: total number of taxa (S), Shannon diversity ($H' = -\Sigma_i p_i (\log_e p_i)$) and Pielou's evenness ($J' = H'/ \log_e S$) (Clarke and Warwick 1994). Secondly the normalised expected number of taxa, calculated after Hurlbert's (1971) modification of Sanders (1968) rarefaction method was used.

Between-habitat (β) diversity: As a measure of β diversity or species turnover the Bray- Curtis similarity between all pairwise permutations of sites was used. The higher the overall similarities are, the lower the β diversity (Magurran 1988).

For α and β diversity, non-parametric Kruskal-Wallis tests and post-hoc multiple comparison (after Nemenyi) were used to test the significance of differences ($p<0.05$) (Sachs 2002). For details on the post-hoc multiple comparisons see Publication III.

Regional (γ) diversity: In order to assess the γ diversity, different indices of diversity were computed. Assuming mainly independent data comparability between primarily single values (H', $E(S_{70})$ and J') for each investigation site jack-knifing was applied (Magurran 1988). Statistical significance was tested using analysis of variance (ANOVA) and post-hoc procedures (Tukey test).

As a second measure of γ diversity, non-parametric estimators of true species richness were computed (Colwell 1997). Values of these true species richness estimators were used as a measure of γ diversity. Detailed information is available in the chapter "materials and methods" in Publication III.

4 Results and Discussion

In the following chapter the results of the investigations are summarised and discussed. A more detailed discussion can be found in the attached publications. Here section 4.1 summarises and discusses general features of the distribution and community structure of the shallow-water (55-160 m) mega-epibenthic communities, while section 4.2 provides examples of spatial patterns of Antarctic benthic shelf communities. Section 4.3 will focus on the biodiversity comparison with high-Arctic shelf mega-epibenthos.

4.1 Distribution and community structure of shallow-water Antarctic mega-epibenthic communities

4.1.1 Hypotheses

On all continents other than Antarctica, animals restricted to shallow waters can disperse continuously along the shelves over long distances. Around Antarctica littoral areas not covered by ice-shelf are scarce and often highly isolated. Does this condition cause a permanent reduction in the dispersion of the shallow-water species, or does a circumpolar relatively homogenous shallow-water fauna exist? Are general conclusions on the role of bridging long distances possible for macrobenthic species?

It is known that benthic shallow-water assemblages in the Antarctic contain a considerable number of species that are highly eurybathic (Brey et al. 1996), whereas others are restricted exclusively to shallow water (Dayton et al. 1970; Gutt 1991).

If such assemblages are not primarily the result of restricted circumpolar dispersion, are they (a) driven by local conditions at shallow depths, or (b) affected by exchange with specific assemblages in adjacent, deeper waters?

4.1.2 Antarctic shallow-water mega-epibenthos: shaped by circumpolar dispersion or local conditions?

The community analyses revealed significant differences between the fauna of all three sites (Fig. 6 and Table 3 in Publication I), Marguerite Bay, Atka Bay and Four Seasons Bank. The faunistic distances between sites and the degree of homogeneity within the sites were similar, with the exception of a more homogenous pattern at Atka Bay.

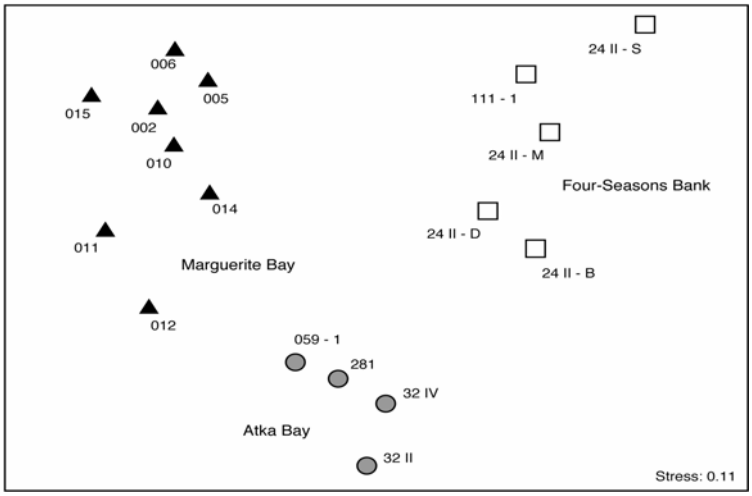


Fig. 6 Nonmetric multidimensional scaling (MDS) ordination based on Bray-Curtis similarity derived from fourth-root-transformed abundance data. *Symbols* represent grouping of stations according to cluster analysis (*S* shallow; *M* middle; *D* deep; *B* fourth part of the transect on the south-west slope)

An important question is whether the faunistic differences reflect the spatial distances between the study sites. Since there are few shallow-water areas to act as stepping stones, colonisation of isolated areas of shallow water could be dispersal limited (Clarke 1996b). The R-statistic values (Table 2 in Publication I) representing faunistic similarities between all sites

are similar to each other, with a slightly higher distance between Marguerite Bay and Four Seasons Bank, which is also shown in the MDS plot. Geographical distances, which represent, at least theoretically, routes of dispersion, differ considerably from this pattern. Atka Bay and Four Seasons Bank are in relatively close proximity, since they are not more than 330 km apart. If distances in space play a dominant role in explaining benthic structures, some of the most abundant species at Atka Bay would also be expected at Four Seasons Bank, because they could be dispersed by the westerly current. Although a depth gradient was found within the data from Four Seasons Bank, differences between all sites were significant. For an exchange of fauna between the two sites in the eastern Weddell Sea and the area west of the Antarctic Peninsula two different routes can be assumed. The first would start in Marguerite Bay, cyclonically following the Eastwind Drift and travelling three-quarters of the entire continent of approximately 11,000 km before arriving in the Weddell Sea. From here dispersion could follow the Weddell Gyre and enter the Bransfield Strait from the region off Joinville Island at the tip of the Antarctic Peninsula (Gordon et al. 2000) leading back to Marguerite Bay. The second route would be dispersal via the Westwind Drift, clockwise from Marguerite Bay. Even by this route, however, the distance to the eastern coast of the Weddell Sea would be 10 times longer than the distance between the two sites in the Weddell Sea.

There is no homogenous shallow water benthos between 60 and 160 m depth, instead different assemblages were found independently of their geographical location and distance from each other.

Benthic assemblages in Antarctica are not shaped significantly by the limitation of long-distance dispersion, caused by the existence of few shallow water areas not being covered by the ice shelf.

Although information on generality in reproduction strategies and early life history is scarce, it seems worthwhile to check some species dominant at our sites for common characteristics regarding the potential to disperse. Several abundant Antarctic invertebrates are short-distance dispersers, either because they reproduce asexually or because they brood their juveniles (Arntz et al. 1994). These reproductive strategies support the local success of single species (Bolker and Pacala 1999), and, if these species become dominant, the community structure can be shaped considerably. Asexual reproduction via budding is prevalent e.g. in the hexactinellid sponge *Rosella racovitzae* (budding type; according to Barthel and Gutt 1992), and brooding seems to be a common feature of reproduction in Antarctic octocorals, e.g. gorgonians (Orejas et al. 2002). The stoloniferous coral *Clavularia* cf. *frankliniana* broods its embryos, and asexual propagation via fission is common (Slattery and McClintock 1997). Long-range dispersion among sessile animals by pelagic planktotrophic larvae, e.g. *Sterechinus neumayeri* and other abundant invertebrates (Bosch et al. 1987, Pearse et al. 1991) supports the coexistence of many species, as has been shown by a spatially explicit simulation model (Potthoff, Johst, Gutt, Wissel unpublished results), and leads to a high capacity to colonise highly disturbed habitats (Poulin et al. 2002).

Modes of reproduction and characteristics of the early life history, e.g. brooding, viviparity or budding, and the consequent patterns of dispersion, of key taxa also shape patterns of species distribution in shallow benthic Antarctic communities.

In order to confirm a certain generality of our results, some species typical or abundant at our sites were checked for their circumpolar distribution: *Rossella racovitzae, Scolymastra joubini, Cinachyra barbata, Monosyringa longispina* (Koltun 1969; Sarà et al. 1992; Gutt and Koltun 1995) and *Synoicum adareanum* (Kott 1969) all have a clear circumpolar distribution and cover a broad depth range. A species reported as common in widely separated areas, but

with less evidence of a widespread circumpolar distribution than those mentioned above is *Sterechinus neumayeri*, present along the Antarctic Peninsula, in the Weddell, Ross and Davis Seas (Pawson 1969). The reason for this might be related to the obvious preference of waters shallower than 300 m (Brey and Gutt 1991). Indeed at Syowa research station, Hamada et al. (1986) described differences in faunal composition at different depths and noted the lack of *S. neumayeri* at 200 m, where bryozoans were very dominant. The hydroid *Tubularia ralphii* has an even more obvious preference for shallow water and, so far, has only been found above 36 m water depth around Antarctica (Dayton et al. 1970, 1974; Propp 1970; Gruzov 1977; Stepaniants 1980; Barnes and Bullogh 1996), although in our study it reached a maximum depth of 104 m at Four Seasons Bank. A similar pattern was shown by the octocoral *Clavularia* cf. *frankliniana*, which is known from the Weddell Sea (this study), South Georgia (Molander 1929) and McMurdo Sound (Dayton et al. 1970, 1974; Slattery and McClintock 1995, 1997), where it is "numerically dominant" between 12 and 33 m and seems to be a true shallow-water taxon. The newly described gorgonian genus *Arntzia* belongs to those taxa that obviously prefer deeper waters, since their shallowest occurrence has been recorded in the Weddell Sea (64 m) and it is known from the Scotia Arc and the Weddell and Ross Seas, but not from other sites in East Antarctica (López-González et al. 2002). Two species that seem to have a limited distribution on the continental shelf are *Oswaldella antarctica*, found at the Antarctic Peninsula (Peña Cantero and Vervoort 1998) and at Four Seasons Bank (this study), and *Schizotricha* cf. *unifurcata*, recorded mainly from sub-Antarctic islands in the Indo-Pacific sector of the Antarctic, as well as in the Weddell Sea (Peña Cantero 1998). Each of the shallow-water assemblages examined in this study has a specific composition, but there is no indication for generally unique faunas at any of these sites, since they represent a mixture of opportunistic species and species with specific environmental demands.

Another reason for the specific faunistic compositions at the three sites could be the considerable exchange with deeper assemblages. In a critical short review of the frequently described "eurybathy" among Antarctic invertebrates, Gutt (1991) suggests that assemblages may also be eurybathic between 160 and 1,180 m. Widespread eurybathy of the Weddell Sea benthos was described by Brey et al. (1996); however, at that time, the shallow sites were not yet known or had not been investigated, and species that occurred elsewhere in shallow waters were not included in the analysis, which reduces the representativity of the results. Use of the 160-m-depth contour as the lower limitation in the present study does not coincide with any clear benthic depth zonation; the depth limitation ensures only that the presence of species restricted to shallow waters is likely to be detected and that assemblages typical of deeper waters are partly represented. Some examples of abundant and typical species have already been discussed. In addition, Hamada et al. (1986) described differences in faunal composition at different depths and noted the lack of *S. neumayeri* at 200 m, where bryozoans were very dominant. Cattaneo-Vietti et al. (1997) mentioned the presence of large beds of *Adamussium colbecki* up to 70-80 m depth, which were abundant, but patchily distributed. Furthermore, Cattaneo-Vietti et al. (2000b) indicated that the bivalves *A. colbecki* and *Yoldia eightsi* seemed to be restricted to relatively shallow water (200 m) at Terra Nova Bay. If the exchange between deeper and shallower benthos is important, then the two sites in the Weddell Sea should be, by far, more similar to each other than is either to the Marguerite Bay site because they are located in an area, where just one quite homogenous community exists on the deeper shelf (Gutt 2000). However, they are not.

Each of the shallow-water assemblages examined has a specific composition, but there is no indication for generally unique faunas at any of these sites.

The Antarctic shallow-water benthos is not shaped by intensive exchange with the deeper fauna, although it is not isolated from these assemblages.

4.2 Spatial patterns of the Antarctic benthos by examples

Research on patterns and processes in benthic communities of the Southern Ocean is of general interest to characterize their structure, to describe their function and to understand their development (White 1984, Arntz et al. 1994, Clarke 1996b). Zonation might be defined as a familiar and ubiquitous organisation of organisms by geography, topography and exposure (Barnes and Brockington 2003). Clear-cut zonation patterns in the form of a serial change in community structure with increasing water depth are a striking feature of intertidal and shallow-water benthic communities on both hard and soft substrata (Clarke and Warwick 1994). Possible causes of zonation patterns are diverse, and may vary according to environmental conditions and ecological demands of assemblages with their specific species composition.

The benthos of the Southern Ocean is influenced by a number of factors including depth, currents, sediments, bottom topography, light or wave energy, ice scouring, competition and predation (Dayton et al. 1974, Dayton 1989, Arntz et al. 1994, Clarke 1996a, 1996b, Slattery and Bockus 1997, Stanwell-Smith and Barnes 1997, Gutt 2000). None of these mechanisms, however, will necessarily give rise to discontinuous bands of different assemblages of species, which is implied by the term “zonation”. Therefore, the more general term “seriation” (zonation with no sharp discontinuities) is perhaps more appropriate to describe continua of changing communities (Clarke et al. 1993, Gherardi and Bosence 2001, Brown et al. 2002). In this context arises the question, what is the structure of Antarctic shallow-water benthic shelf communities at intermediate scales?

4.2.1 Horizontal seriation

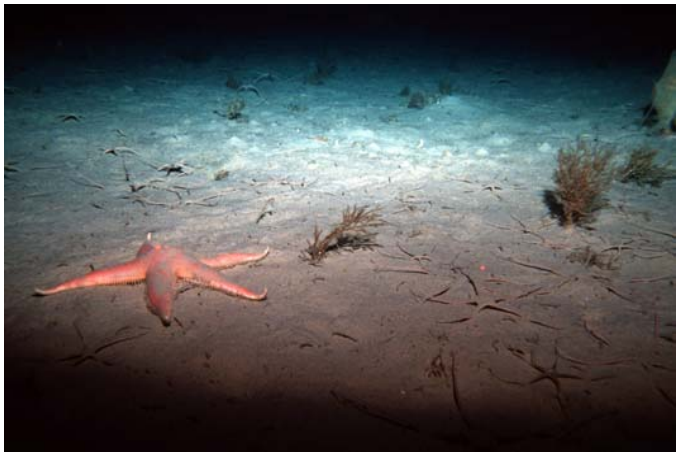
Specific seriation patterns of benthic ecosystems may be caused by both abiotic conditions (depth, substratum, habitat, bottom topography, sedimentation, oceanography, disturbance) (Dayton et al. 1970, 1994, Gallardo 1987, Barnes et al. 1996, Gutt 2000) and by biotic factors (competition, predation, recruitment) (Rowe 1981, Arntz et al. 1994, Clarke 1996a, 1996b).

Stations with the poorest seriation (Table 1 in Publication II), e.g. stn 015, 059-1, and 32IV belong to those with the smallest range of species or faunal-heterogeneity in combination with intermediate values for species turnover (median of Bray-Curtis values) (Fig. 7 in Publication II). This shows that along the 150 m standardized transects neither a patchwork of different assemblages nor a gradual change in assemblages exists, instead the fauna is quite homogenous. This phenomenon was observed locally in all three areas of investigation. Interestingly, this includes two stations (059-1 and 32IV) which are situated close (<0.5 km) to the ice shelf coast, where, due to a continually changing environment, greater differences in benthic communities can be expected than elsewhere or at different spatial scales (Barry and Dayton 1988, Gutt 2000).

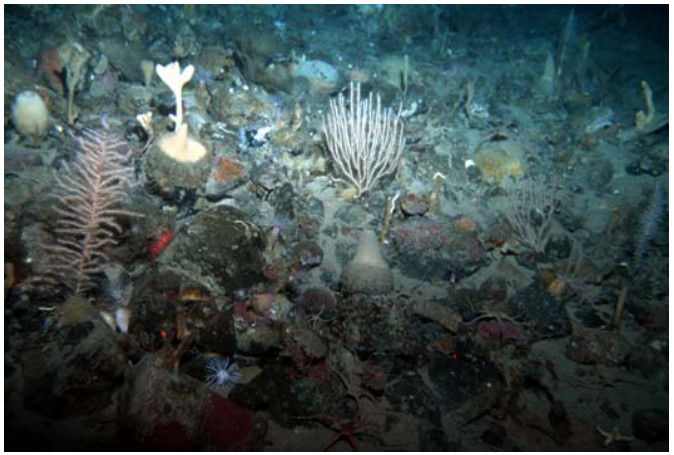
Discontinuity in the macro-epibenthic assemblages may correspond to a sharp change in local bottom topography (Pérès 1982). Some of the stations analysed in Marguerite Bay displayed abrupt changes in the bottom topography, e.g. stn. 010 (Fig. 7). Soft-bottom sediments with valleys and crests, drop stones, and biogenic substrata (e.g. scallop shells of *Adamussium colbecki*) were observed along this transect.

An exceptional result in terms of species turnover is that of stn 010 (Fig. 7 in Publication II), with a high heterogeneity, whilst the IMS value and its significance level were intermediate

a)



b)



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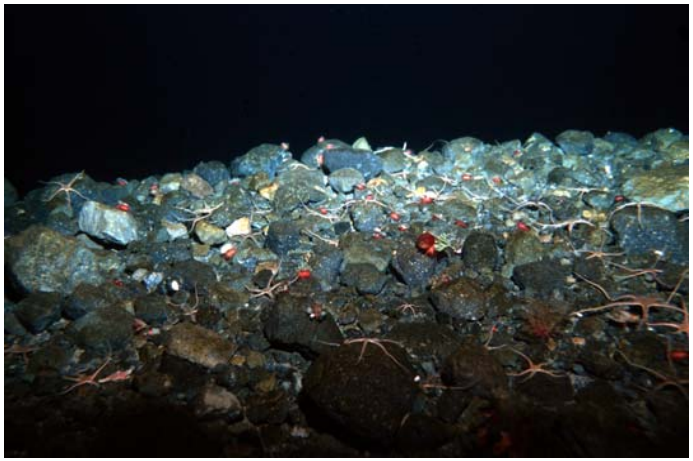

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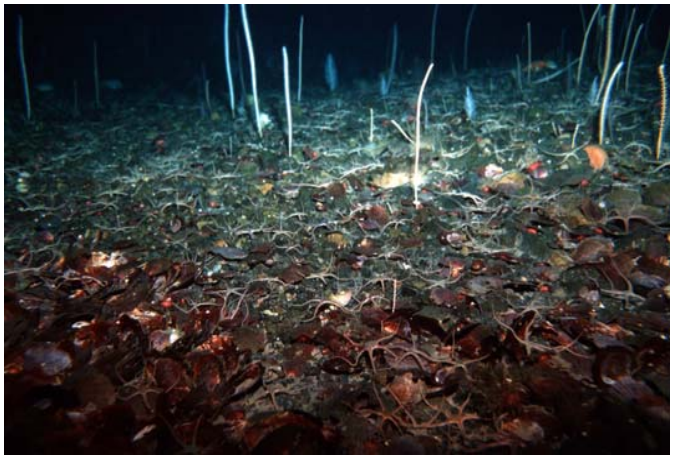
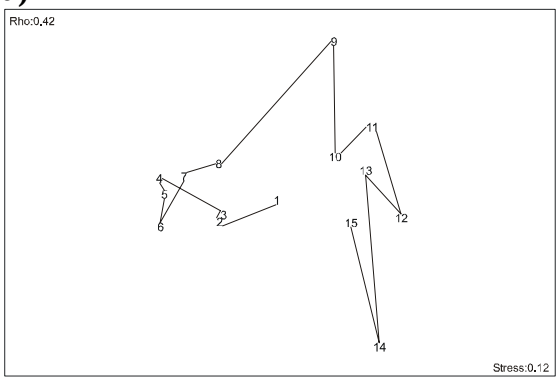


Fig. 7 Horizontal seriation in the Bellingshausen Sea (Marguerite Bay, stn 010): photographic representation of the substrata of the subsamples. **a)** Sand bottoms, with valleys and crests, (80 m). **b)** and **c)** mixture of sand with pebbles and cobbles, (77 and 73 m). **d)** Shell-beds of *Adamussium colbecki*, (70 m).

Stn 012

a)



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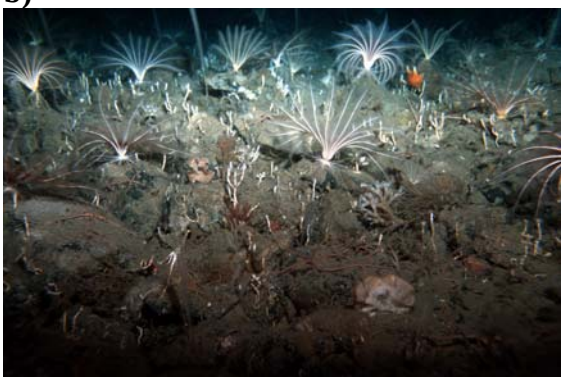

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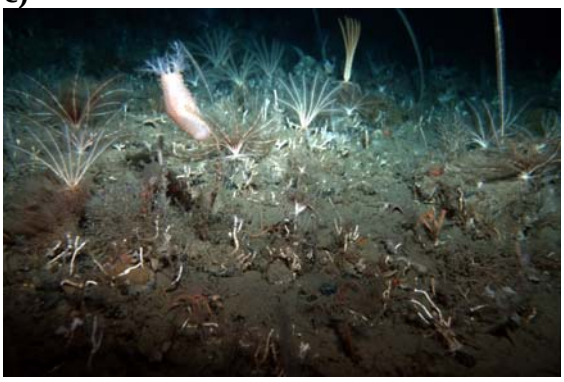
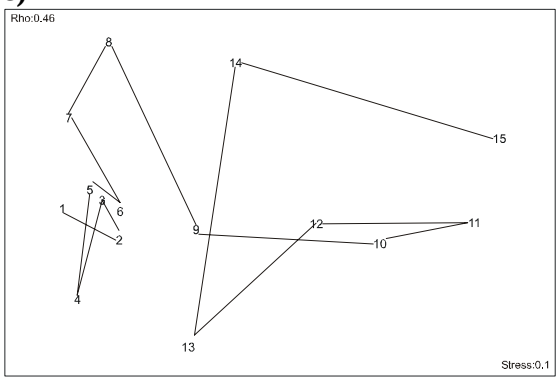


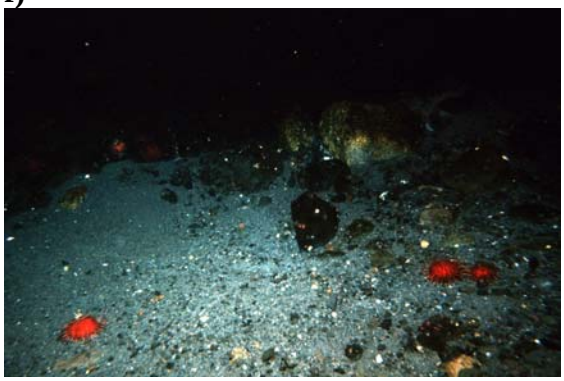
d)

Stn 24II shallow

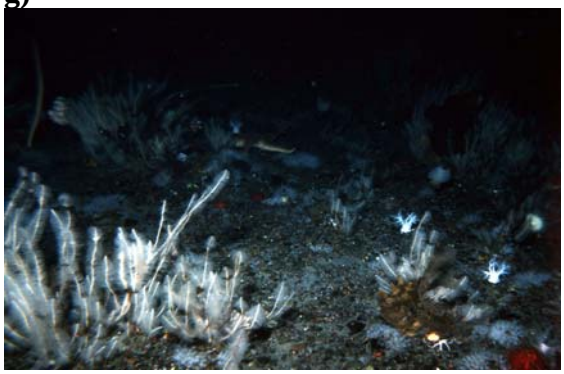
e)



f)



g)



h)

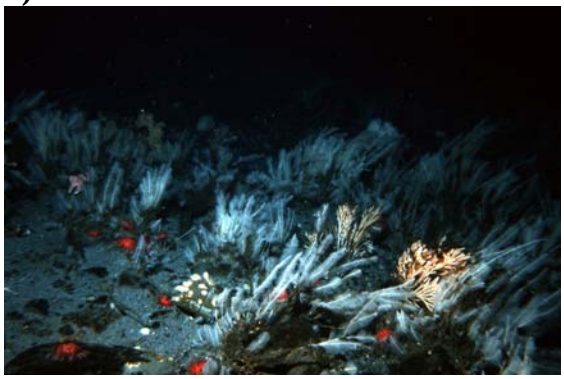
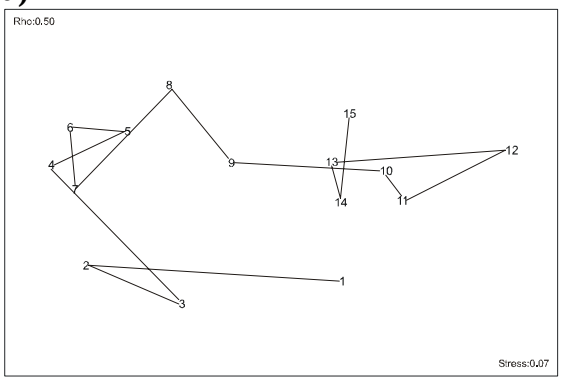


Fig. 8 Horizontal seriation in the Bellingshausen (stn 012) and Weddell Seas (stn 24II shallow), photographic representation of some of the outliers in the seriation. **a)** and **e)** MDS ordination. *Stn 012*: **b)** and **c)** show part of the community structure present at the majority of the subsamples, with high abundances of the sedentary Polychaeta sp.1 (106 m). **d)** Represents outliers of the seriation (subsamples 9 and 14) showing low abundances of the Polychaeta sp.1 (102 m). *Stn 24II shallow*: **f)** Ice scour, with low abundances of *Oswaldella antarctica* (Hydrozoa) (subsamples 7-8) (58 m). **g)** and **h)** Display differences in abundances of *O. antarctica* and sediments between different subsamples (60 and 59 m).

Stn 24II middle

a)



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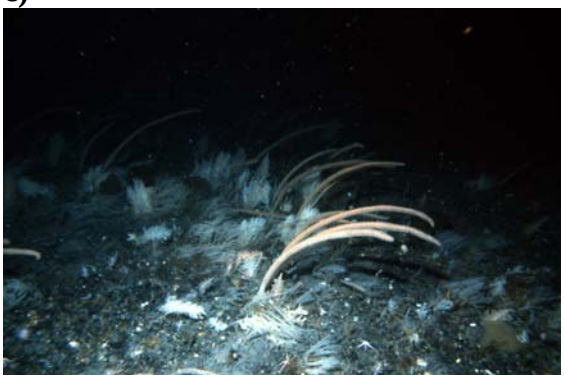

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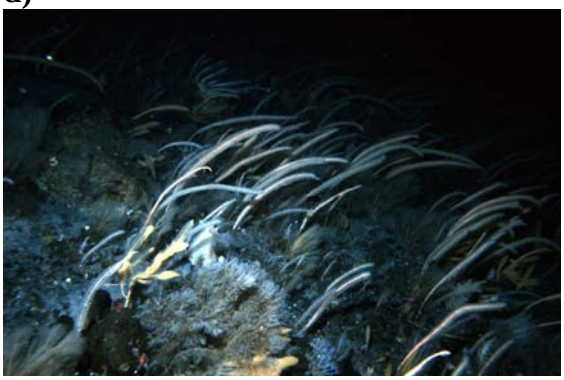
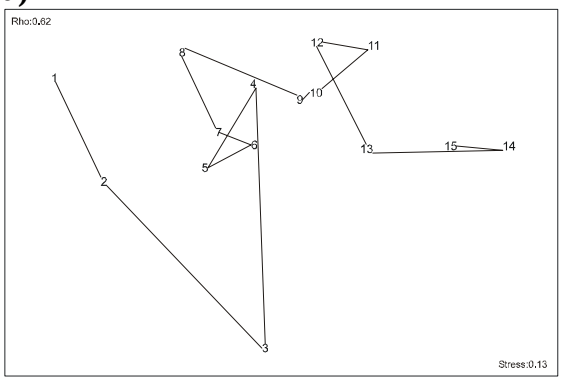


Stn 24II deep

a)



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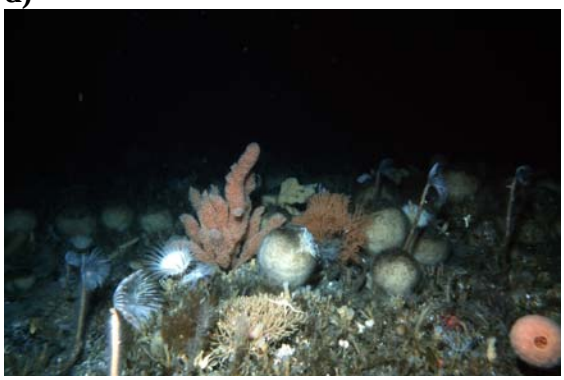


Fig. 9 Horizontal seriation in the Weddell Sea (Four-Seasons Bank), photographic representation of some of the outliers in the seriation. **a)** MDS ordination. *Mid-depths*: **b)** Assemblages of gorgonians present where strong currents are absent (subsamples 1-3), (120 m), conversely, assemblages of subsamples 4-12 (**c** and **d**) present at sites characterized by strong currents, (118 and 95 m). *Deep sites*: **b)** Displays subsample 3, with absence of *C. barbata* (Demospongiae, 129 m), which is present at subsamples 1-2 (**c** and **d**), (128 and 130 m).

(Table 1 in Publication II). Here obviously changing environmental conditions at different levels shape a heterogeneous megabenthos. The fauna seems to exhibit both a gradual change in taxa composition and, superimposed, a faunal patchwork shaped by discrete impact independently of the locality on the transect.

Stations with the poorest seriation belong to those with the smallest range of species or faunal-heterogeneity but with intermediate values for species turnover.

Discontinuity in the mega-epibenthic assemblages may correspond to a sharp change in local bottom topography.

Four transects, one from the Marguerite Bay (stn 012) (Fig. 8a-d) and three from the Four Seasons Bank (stn 24IIA-shallow, 24IIA-middle, 24IIA-deep) (Fig. 8e-h and 9), show relatively good faunal seriation, though, never high values close to 1.0 (Table 1 in Publication II). The latter transects have broad ranges of species turnover values (Fig. 7 in Publication II). Because of the mathematical nature of the IMS this combination of median and value range can be found if an existing seriation is occasionally interrupted. At both sides of the Four Seasons Bank the most obvious disturbance agent is iceberg scouring, a process which also leads to the heterogeneity within the two groups of subsamples, SW-slope and NE-slope, the latter including one subsample with an extreme faunistic composition. The same was observed in the "Top" group where additional disturbance, such as wave action, an especially strong exposure to tidal and other currents, changes in daylight and a more intensive ice impact due to shallow water depth is obvious. The fact that nevertheless a significant seriation existed might be due to the small but not avoidable depth gradient within each depth stratum (=transect, 24IIA-shallow, 24IIA-middle, and 24IIA-deep), causing gradients in ecologically relevant conditions as also observed at a larger spatial scale discussed below. In contrast to all the other results discussed above stn 012 in Marguerite Bay has a relatively

high median value of species turnover, with a narrow range of corresponding single values (Fig. 7 in Publication II). This can be explained by an obviously very good seriation, however, without a very clear faunal difference between the beginning and the end of the transect and not being considerably interrupted. Furthermore there was no indication of any change in the abiotic environmental conditions. This is confirmed by the horseshoe-shaped MDS plot, a pattern which is typical of temporal succession rather than for the spatial structure found here.

Stations with relatively good faunal seriation displayed broad ranges of species turnover.

Seriations are occasionally interrupted by disturbances such as ice scouring.

Significant seriations observed at Four .Seasons Bank might be influenced by the small but not avoidable depth gradient within each depth stratum, causing gradients in ecologically relevant conditions.

4.2.2 Depth zonation

Clear zonation according to depth has been observed by different authors (Rowe and Menzies 1969, Dayton et al. 1970, 1974, Carey et al. 1975, Piepenburg and Schmid 1996, Mayer and Piepenburg 1996). Vertical distributions of benthic communities (0-150 m) in Terra Nova Bay (Ross Sea) (Cattaneo-Vietti et al. 2000a) displayed some similarities with the pattern observed at Four Seasons Bank. At depths between 2 and 70 m the sea urchin *Sterechinus neumayeri* is also abundant; below this depth range (up to 150 m) a complex community of sponges and anthozoans characterize the area. The sponge community living at Four Seasons

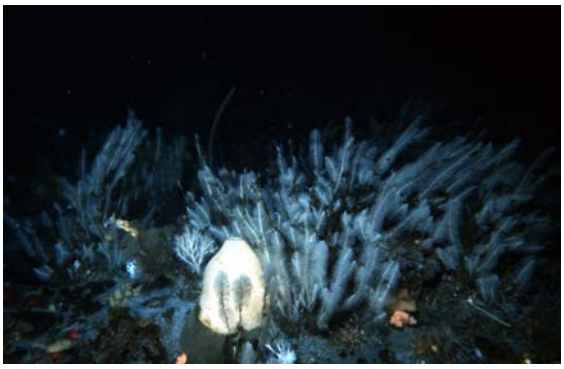
Bank is quite similar to those found at McMurdo Sound: mixed and glass sponge communities (Bullivant 1967, Dayton et al.1974), but at both sides of the bank (NE and SW "slopes") high abundances of single species like *Cinachyra barbata*, *Stylocordyla borealis* (round type), *Tedania tantula*, *Monosyringa longispina*, *Polymastia invaginata*, *Polymastia isidis* are remarkable.

In general, the Four Seasons Bank seems to comprise several faunal assemblages which combines a clear depth gradient and a zonation with discrete assemblages (Fig. 8 and 9 in Publication II). Special environmental conditions are originated due to the topography of the bank. Strong currents and a generally enhanced variability on banks have been observed frequently (Genin et al 1986; Beckmann 1999). Hydroids (*Tubularia ralphii*, *Oswaldella antarctica*, *Corymorpha parvula*, Hydrozoa sp.8 and *Corymorpha* sp.1) and anthozoans (*Clavularia cf. frankliniana*), especially gorgonians (*Ainigmaptilon antarcticum*, *Primnoisis* spp., *Thouarella* spp., *Dasystenella* sp., *Fanyella* spp.), were well represented (Fig. 10 and Fig. 10a-c in Publication II). Some of these species are described as "macro"- and microphagous" suspension feeders whose feeding strategies imply that sediment might be resuspended e.g. by the effect of currents (Orejas et al. 2001, 2003) and that other methods than active filtration (e.g. gravitational deposition, direct interception) may also occur (LaBarbera 1984). In this context, strong currents seem to be an advantage for the establishment of this group of organisms because these currents supply them with food (Genin et al. 1986, Rogers1994).

Four Seasons Bank seems to comprise several faunal assemblages which combines a clear depth gradient and a zonation with discrete assemblages.

a)

b)



c)

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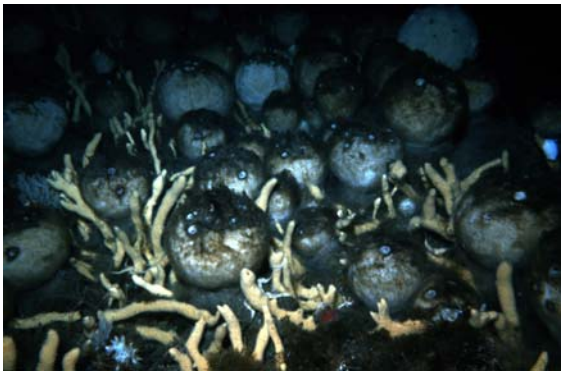

Depth zonation and diversity values (Fig. 10 and Fig. 12 in Publication II) observed appear to be strongly influenced by the nature of the substratum (cf. Pérès 1982, Kirkwood and Burton 1988, Hecker 1990, Simboura et al. 1995, Nonato et al. 2000). The lowest values were displayed in shallow areas at the northern site of the bank where drop stones and boulders were the main substrata. This type of substrata favoured epilithic organisms or species that need a form of anchorage for their settlement; e.g. the octocoral *Clavularia* cf. *frankliniana* forms encrusting colonies that cover a great part of the stone (Gili et al. 1999) and the hydroid *Tubularia ralphii* forms creeping colonies on stones (Stepaniants 1980).

Fig. 10 Depth zonation at Four Seasons Bank (eastern Weddell Sea). *Top of the bank* **a)** *Clavularia* cf. *frankliniana* (Octocorallia), *S. neumayeri* (Echinoidea), (60 m). *Mid-depths* **b)** *Oswaldella antarctica* (Hydrozoa), *Polymastia invaginata* (Demospongiae), (68 m) and **c)** *Primnoella* spp. (Gorgonacea, 95 m). *Deep sites* **d)** Sponge assemblages: *Cinachyra barbata* and "Yellow branches" (Demospongiae, 135 m).

The complex morphology and architecture of specific organisms (e.g. sponges, gorgonians, bryozoans, ascidians) offer a variety of secondary habitats providing favourable conditions for epibiotic species (Gutt and Schickan 1998). This might explain high values of diversity and number of taxa observed at both sides of the bank (NE and SW "slopes"), where sponges were abundant (Fig. 10d-f and 11 in Publication II). Sponges provide the most fascinating of these secondary habitats in Antarctica (Arntz et al 1997, Gutt and Schickan 1998), being associated with a large number of organisms that exhibit epibiotic behaviour (Gutt and Schickan 1998). These associations generate a variety of "multi-storied habitats" and living substrates provide additional ecological niches (Gutt 1996) (Fig. 11). Furthermore, differences in current regimes at both sides of the bank (Fahrbach et al. 1992, Dijkstra 2000) might explain faunistic differences found between the northeast and southwest "slopes".

Fig. 11 "multi-storied" habitats: *Psolus* spp. (Holothuroidea), *Astrotoma agassizii* (Ophiuroidea) and crinoids on gorgonians.

Depth zonation and diversity values observed appear to be affected by the nature of the substratum.

Low values of diversity were displayed in shallow areas of Four Seasons Bank where boulders and gravel were the main substrata.

High values of diversity and number of taxa were observed at both sides of the bank, where complex morphology and architecture of specific organisms, especially sponges, provided secondary habitats for epibiontic species.

Differences between the Northeast and Southwest "slopes" were found, with a higher heterogeneity at the Northeast "slope"

In general these findings show, that despite the isolated nature of the Antarctic ecosystem, each detailed look at mega-epibenthic assemblages provides more insight into a high complexity of processes behind spatial structures. Our results do not only provide evidence that the high Antarctic benthos is not homogenous as indifferently stated some decades ago. They also show that the opposite, "all patterns can occur everywhere" as stated in some more advanced studies (Gutt and Piepenburg 2003), is not a general phenomenon if results refer to comparable spatial scales.

Different kinds of patterns are identifiable: a locally limited typical fauna, a patchwork of assemblages as well as continuous faunistic gradients. Combinations of these three scenarios are possible or must even be considered as the rule.

4.3 Biodiversity at different spatial scales: Parallelism with the Arctic?

Measures of species diversity are central to many aspects of ecology and conservation (Whittaker 1960, Magurran 1988, Gaston 1996, Gray 2000). The concept of biological diversity as the "variety of living organisms" cannot be summarized by a single measure (May 1994, Ellingsen 2001) and there is also no single correct scale at which to view ecosystems (Levin 1992). The concept of diversity expresses something more than the notion of the effective number of species present (Hill 1973, Williamson 1997). Distributions of species and community differences should be taken into account in addition to species diversity when measuring marine biodiversity (Ellingsen 2001).

Gray (2001) concluded that two basic considerations have to be taken in account when comparing the Arctic with the Antarctic: age and area. The benthic fauna of an area such as the Southern Ocean cannot be viewed in isolation, and it is pertinent to ask how the present Antarctic fauna is related to faunas elsewhere (Clarke 1996b). Following this argument a reasonable approach is to study the faunistic and environmental parallelism with the Arctic. The Arctic and Antarctic benthic faunas have been compared previously by George (1977), Knox and Lowry (1977), White (1984), Dayton (1990) and Piepenburg et al. (1997), and all have indicated high species richness and diversity in the Southern Ocean. Recent studies on Antarctic benthic diversity (Clarke and Johnston 2003, Gutt et al., *in press*) have been made in order to get a better approach to the existent taxa and their number of species. With this background, a comparison between polar shelves was made in order to answer the following questions: (a) Is the mega-epibenthos inhabiting the Antarctic shelf in the Weddell and Bellingshausen seas really more diverse than that of the Arctic?, (b) Does shallow-water polar mega-epibenthos exhibit a higher heterogeneity than the benthos on the deeper shelves?

Hypotheses and results are presented in an overview in Table 1, in which the comparisons between the Arctic and the Antarctic as well as shallow and deep polar samples at different spatial scales are shown diagrammatically (Fig. 2, 3, 4,5 and details on the hypotheses in Publication III). Here only significances between comparable units are depicted, e.g. between shallow and deep assemblages within one investigation site or between shallow sites but not for example between shallow Antarctic and deep Arctic stations or vice versa.

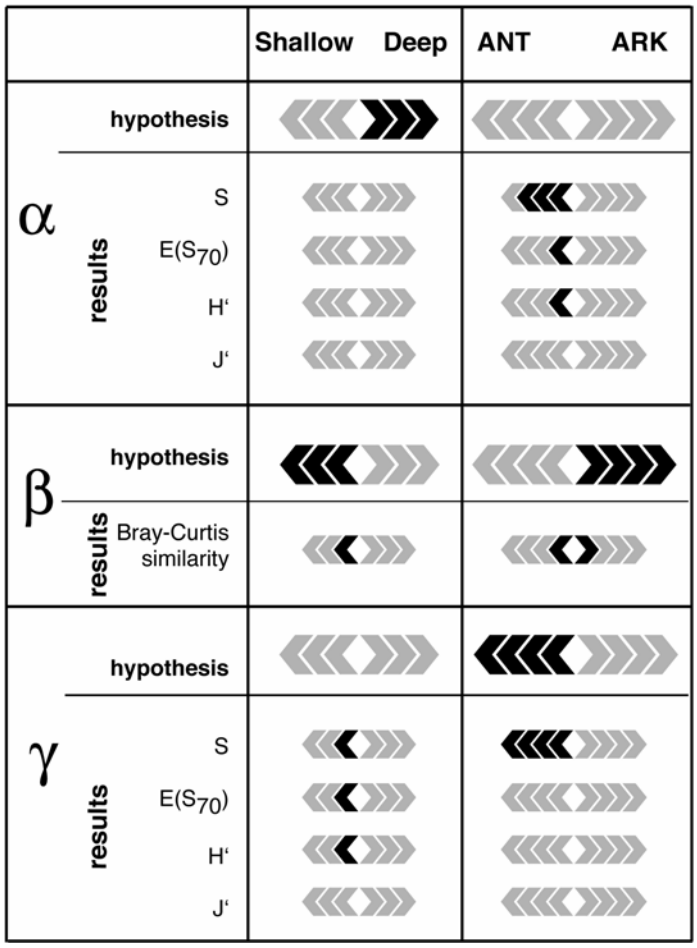

Table 1 Schematic representation of the results and hypotheses tested for within-habitat (α), between-habitat (β) and regional (γ) diversity at shallow (35-150 m) and deep (160-585 m) sites and for Antarctic (ANT) and Arctic (ARK) regions. For details on the hypotheses see introduction in Publication III. S: number of taxa; $E(S_{70})$: rarefaction richness estimator; H': Shannon diversity; J': Pielou's evenness. The tone intensity of the arrows indicates the trend of the direction into which the hypothesis goes.

4.3.1 Gamma and beta diversity

Diversity, often reduced to pure species numbers, is regulated at the regional (gamma) scale mainly by historical processes (Crame and Clarke 1997, Gray 1997). Consequently, dissimilarities in the evolution of Arctic and Antarctic faunas (Dayton 1990) have to be considered, when trying to understand patterns we observe today (Clarke 1996b). Environmental stability over evolutionary time was identified by Sanders (1969) as the main driver to foster specialization e.g. in the deep sea since species are able to adapt to each other and require less effort to adapt to the environment. The resulting effect is that many species

with narrow, almost non-overlapping niches coexist (Grassle and Sanders, 1973). In this convincing concept, however, the role of large, primarily geomorphological disturbances is ignored. Pianka (1978) also considered competition as an important evolutionary force that has led to niche separation, specialization and diversification. In addition, Dayton and Hessler (1972) pointed out the importance of continued biogenic disturbance as a significant factor in maintaining high diversity. They argued that as an effect of disturbance, resources might become less limiting and as a result the probability of competitive exclusion is reduced.

Our results show that both Antarctic study sites are richer in the number of mega-epibenthic taxa than the Arctic. This cannot be explained exclusively by either stability or disturbance. An increase in species number as a result of environmental stability during discrete periods such as interglacials and glacials according to Sanders (1969) was regularly and irregularly interrupted by climatic shifts with enormous consequences for the benthos (Clarke and Crame 1989). In this context vicariance can have a great importance (Clarke and Crame 1992), since speciation may occur as a result of geographic or ecological separation and subsequent isolation of portions of an original population (Pielou 1979, Barton 1990, Myers and Giller 1990). The rate of resulting speciation may vary systematically with conditions that promote reproductive isolation between populations and that enhance the rate of evolution (Ricklefs 1987).

However, both polar regions generally experienced the same conditions. One major difference in this context might be the fact that in case of large-scale marine warming and cooling the Arctic fauna had a chance to migrate longitudinally, and consequently genetic exchange among populations was not blocked as much as in the Antarctic by large ice extensions. We do not claim for a complete knowledge of all evolutionary relevant factors but it seems to be logical that their characteristic combination and specific details may have

led to the higher species number in the Antarctic. This includes not only environmental conditions but also positive and negative interspecific interactions, such as development of commensalism, e.g. epibiotic life (Gutt and Schickan 1998) as well as well balanced concurrence and competition (Dayton et al. 1974). In addition the Arctic is younger as a cold environment, what could probably explain its lower species richness since there may have not been enough time and environmental stability (Grassle and Sanders, 1973) for the establishment of an extensive species component (Gray 2001). Indeed different authors (Vermeij 1991, Dunton 1992) have remarked that the Arctic marine ecosystem is in an evolutionary sense still facing colonization.

Not many theories exist about evolutionary processes triggering a high numerical equitability among species or, alternatively, a high dominance of single species. Our results show that at a large spatial scale species numbers are not related to dominance patterns; otherwise any of the variables including equitability, $E(S_{70})$, H', or J' would also be higher in the Antarctic. Obviously the above-mentioned complexity of forces does not lead to a composition of species with a higher numerical equilibrium. In the older Antarctic as well as in the younger Arctic communities (Knox and Lowry 1977, Dayton 1990, Gray 2001) both, rare and dominant species seem to perform independently a successful adaptive strategy over evolutionarily relevant periods.

Both Antarctic study sites are richer in the number of mega-epibenthic taxa than the Arctic.

Not only environmental conditions but also positive and negative interspecific interactions, such as development of commensalism, e.g. epibiotic life as well as well balanced concurrence and competition have led to the higher species number in the Antarctic.

To compare the faunas of shallower and deeper shelves in the light of evolutionary processes is only worthwhile if a clear depth zonation exists as found in the Arctic (Piepenburg and Schmid 1996). In the Antarctic except for a zone exposed to permanent sea-ice disturbance a large proportion of the fauna is eurybathic (Brey et al. 1996). In addition, also a true shallow-water fauna exists (Gutt 1991). Generally, it can be stated that over both evolutionarily and ecologically relevant time scales the environment in shallow-water systems is more heterogeneous and dynamic than in deeper systems, an assumption on which some of our hypotheses were based. In the Arctic the deeper site was slightly poorer in species and species turnover (beta-diversity) indicating a lower habitat heterogeneity compared to shallower habitats. In the Arctic only the shallow depth stratum is affected by iceberg scouring. Consequently, the difference between shallow and deeper sites can reflect among other locally changing ecological conditions this specific impact. However, it is not yet quantitatively investigated at this study site.

In the Antarctic all regional species numbers in the shallow sites were higher than in deeper ones including one significant difference, but in contrast to the Arctic this cannot be explained by a higher species turnover. This might indicate a different origin or colonization history of shallow and eurybathic species. At the deeper stations a high proportion of eurybathic species occurs as well as in the shallow sites where, however, additional species restricted to shallow waters are present. The deeper species could colonize the circumpolar continental slope during ice ages. The shelf, however, was mainly covered by overlying shelf ice (Anderson et al. 1980, Anderson 1991, Harris and O'Brien 1996) and many populations, species, and their assemblages restricted to shallow water were separated and evolved during these periods in sparse Antarctic shallow water refuges. At the beginning of interglacials these mixed among each other and with the deeper species on the continental shelf primarily without much competition and, thus, contributed to the high regional species richness.

Concerning the comparisons between species turnover (beta diversity) in the Arctic and Antarctic samples no systematic trends were found since in one case the Arctic and in another the Antarctic study site had a significantly higher species turnover. As with the comparison between depth strata this indicates that rather locally changing ecological conditions within the study sites than differences in long-term evolutionary processes between both polar regions affect species turnover patterns.

In the Antarctic all regional species numbers in the shallow sites were higher than in deeper ones including one significant difference, but in contrast to the Arctic this cannot be explained by a higher species turnover.

No differences were found in species turnover between the Arctic and Antarctic, since in one case the Arctic and in another the Antarctic study site had a significantly higher species turnover.

Similarly to the comparison between depth strata this indicates that rather locally changing ecological conditions within the study sites than differences in long-term evolutionary processes between both polar regions affect species turnover patterns.

4.3.2 Alpha diversity

Why did the results from both comparisons Arctic versus Antarctic, shallow versus deep not follow our hypotheses? We cannot imagine that recent ecological conditions in small areas of 100 m^2 or, in other words, the carrying capacity for alpha diversity differ in a way that the presence of more species is favoured in one of the two polar regions by the presence of a higher number of microniches. Generally, small-scale coexistence of many species is also supported by a fast dispersal through reproductive stages (Holmes and Wilson 1998, Amarasekare and Nisbet 2001, Shurin and Allen 2001). However, despite the fact that

recently for some abundant species meroplanktonic larvae have been discovered (Pearse et al. 1991, Stanwell-Smith et al. 1999, Gambi et al. 2000b, 2001), environmental conditions in the Antarctic seem to favour direct development (Poulin et al. 2002). Nevertheless, at the local spatial scale species numbers were higher in the Antarctic. We believe that this is due to the clearly higher regional diversity. This includes the occupation of specific small-scale niches, which, however, must be primarily considered as a large-scale phenomenon. Such adaptive strategies evolved in the entire Antarctic as the above mentioned epibiotic life or any traits in the early life history e.g. preference of generally poorly sorted sediments which are so far totally undiscovered.

Another reason for the higher local species numbers in the Antarctic could be differences in natural disturbances such as predation pressure or iceberg scouring (Lewis and Blasco 1990, Gutt 2000, Gutt and Starmans 2001). If in the Antarctic most, if not all, sites investigated did not return to an advanced stage of equilibrium they could harbour a maximum diversity according to the intermediate disturbance hypothesis (Huston 1979). The impact of iceberg scouring on polar benthic communities can play an important role in both hemispheres (Gutt et al. 1996, Conlan et al. 1998, Gutt 2001), however, studies focussing on smaller spatial scales are, at least for the Antarctic, necessary to detect corresponding effects (Gutt and Piepenburg 2003). If the intermediate disturbance hypothesis can be applied the question remains open, whether in the Arctic disturbances are less frequent or more effective and thus species numbers are reduced. In the latter case we would expect also a higher evenness in the Arctic, which we did not find. It is also still open whether the Antarctic benthos is still in a non-mature stage after the last glaciation (Gutt 2000) and whether in the future due to competition less robust species will get extinct at least at the local scale.

At the local spatial scale species numbers were higher in the Antarctic compared to the Arctic, what might be a reflection of a clearly higher regional diversity.

Natural disturbances such as predation pressure or iceberg scouring are another reason for the higher local species numbers in the Antarctic.

5 Publications

The publications of this thesis are listed below and the contribution from each author in the different papers is also outlined.

Publication I:

Juana M. Raguá-Gil, Julian Gutt, Andrew Clarke, Wolf E. Arntz

Antarctic shallow-water mega-epibenthos: shaped by circumpolar dispersion or local conditions?
*Marine Biology, in press**

The original idea for this paper was developed by the first two authors. I conducted the video and data analyses and wrote the first version of the manuscript which was then improved in cooperation with the co-authors.

Publication II:

Juana M. Raguá-Gil, Julian Gutt, Wolf E. Arntz

Antarctic mega-epibenthos: horizontal seriation and depth zonation by examples

The first and second author discussed the conceptual frame of this publication. The video and data analyses were conducted by the first author. After writing the first draft of the manuscript, I discussed and revised it with the co-authors.

Publication III:

Juana M. Raguá-Gil, Julian Gutt, Andreas Starmans, Wolf E. Arntz

Differences in mega-epibenthic diversity on polar shelves at different spatial scales

I did the video analyses for the shallow-water areas in the Antarctic. Preview video analyses of data for the Arctic and deep areas of the Antarctic was performed by the third author. I conducted all data analyses and wrote the first version of the manuscript which I then revised in close cooperation with the co-authors.

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Publication I

Antarctic shallow-water mega-epibenthos: shaped by circumpolar dispersion or local conditions?

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Antarctic shallow-water mega-epibenthos: shaped by circumpolar dispersion or local conditions?

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Abstract The mega-epibenthos of two different geographic areas, Antarctic Peninsula and the high Antarctic (eastern Weddell Sea), were investigated using underwater video. The distribution of the marine fauna at shallow depths between 55-160 m in these two areas was investigated to determine whether there are any zoogeographic differences at community level. A total of 237 taxa represented by 85,538 individuals was identified. Multivariate analyses revealed significant faunal differences between northern Marguerite Bay (western Antarctic Peninsula) and the stations from the Weddell Sea, Atka Bay and Four Seasons Bank. Echinoderms, especially ophiuroids, dominated Marguerite Bay, bryozoans and ascidians were abundant at Atka Bay, and hydroids and gorgonians were well represented at Four Seasons Bank. These clear differences can mainly be explained by the influence of local environmental conditions that are probably the primary feature responsible in shaping the Antarctic shallow-water epifauna and not an intensive exchange with larger depths or a limited dispersion due to scarce and isolated shallow areas. In addition, modes of reproduction and characteristics of the early life history (e.g. brooding, viviparity or budding) of key taxa may also shape patterns of species distribution in shallow benthic Antarctic communities.

Introduction

The origin and evolution of the Antarctic benthic fauna have long been discussed in the literature (Lipps and Hickman1982; Clarke and Crame 1989, 1992, 1997). The faunas of the Antarctic Peninsula and of the high-Antarctic Weddell Sea have long been considered to belong to different zoogeographical regions (Hedgpeth 1971). These two areas separated from each other by ca. 2,160 km, are characterised by strong seasonality, with changing light regimes, ice coverage (Gutt 2000), primary production, sedimentation (Arntz et al. 1992), but relatively constant physical conditions (Klages 1993; Klages et al. 1995). However, these two regions differ in one striking aspect that is generally relevant to the benthos, namely, that the Antarctic Peninsula has a true coast and, thus, true littoral areas are common. In contrast, > 95% of the coastline and near-shore region of the high-Antarctic is covered by floating or grounded ice; thus, deep waters (>150 m) predominate and consequently shallow areas are scarce (Drewry 1983; Gutt 2000). In the Weddell Sea, two shallow sites with water depths between 55 and 160 m are known: the inner parts of Atka Bay and a recently discovered shallow bank off Four Seasons Inlet north-east of Kapp Norvegia. This bank seems to host a faunal assemblage, which differs from that of well-investigated, adjacent, deeper waters.

With this background, the current study centred around the following hypotheses and questions:

1. On all continents other than Antarctica, animals restricted to shallow waters can disperse continuously along shelves over long distances. Around Antarctica littoral areas not covered by ice-shelf are scarce and highly isolated. Can this condition cause a permanent reduction in the

dispersion of the shallow-water species, or does a circumpolar, relatively homogenous, shallow-water fauna exist? Are general conclusions on the role of bridging long distances possible for macrobenthic species?

2. It is known that benthic shallow-water assemblages in the Antarctic contain species that are highly eurybathic (Brey et al. 1996) or restricted exclusively to shallow water (Dayton et al. 1970; Gutt 1991). If such assemblages are not primarily the result of unrestricted circumpolar dispersion, are they:

a. driven by local conditions at shallow depths, or

b. affected by exchange with specific assemblages in adjacent, deeper waters?

The general approach for this study was to determine whether zoogeographic patterns at the community level could be detected from which conclusions could be drawn. We employed video techniques that are highly effective for marine ecological studies at large spatial scales, especially for work with the mega-epibenthos, because of their high spatial resolution (Clarke 1996a), which permitted the determination of abundances for each square metre separately. Recent advances in remotely operated vehicle (ROV) technology allowed the recording of a continuous stream of images with resolution and colour saturation sufficient to identify the fauna and determine fine-scale substrate characteristics (Malatesta et al. 1992).

This study is a contribution to the SCAR (Scientific Committee on Antarctic Research) programmes EASIZ (Ecology of the Antarctic Sea Ice Zone) and EVOLANTA (Evolution in the Antarctic), which together provide a framework for research on the evolutionary history and biology of Antarctic biota.

Materials and Methods

Study sites and sampling

A total of 17 sea-bed video-observation transects were conducted at 14 stations using a ROV ("Sprint 101"), at shallow depths between 55 and 160 m. The sampling locations are shown in Fig. 1. With the exception of station (stn) ANT XIII, 24II (see below), each single station comprised a video transect lasting approximately 60 min. The length of the transect was determined by the drift of the ship and the width (ca. 0.5 m) by two parallel laser beams, which also acted as a scale on the image. It was attempted to select from the complete transects a standardised section of 400 m length with the best optical quality. This length could not be obtained at all stations, leading to an average area covered of 174 m^2.

In the first investigation area, the Weddell Sea, video records were taken during the expeditions ANT XIII/3, ANT XV/3 and ANT XVII/3 of the German R.V. “Polarstern” (for details on the expeditions see Arntz and Gutt 1997, 1999; Arntz and Brey 2001). One study site is situated in and west of Atka Bay, with one station having a minimum water depth of 55 m; here the sea-floor rises continuously, in a width of approximately 5 km, to the ice-shelf coast, where the ice is locally in contact with the sea-floor (Grosfeld et al. 1989). The other site is a shallow bank off Four Seasons Inlet (71°07,5'S; 11°28'W) north-east of Kapp Norvegia. This bank is approximately 1.7 km long in its north-west-south-east extension and, on average, 320 m wide; it rises from a plateau at 170 m depth to 60 m depth at its shallowest part. Its north-eastern slope is relatively steep over the complete depth-range from approximately 150 to almost 60 m. Here, the complete ROV station (ANT XIII, stn 24II) was split into four different transects: on the north-

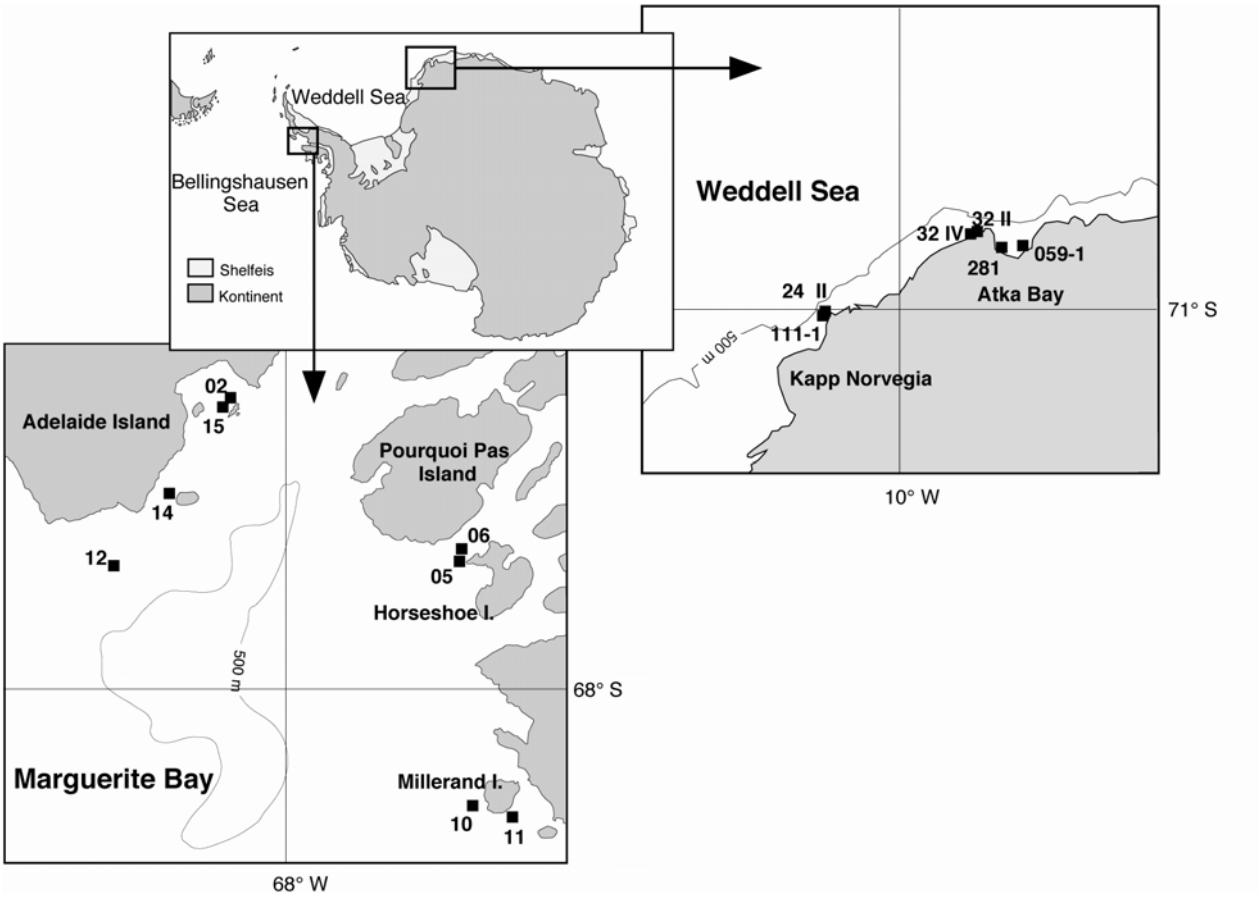

Fig. 1 Areas of investigation: Marguerite Bay (Antarctic Peninsula) and Weddell Sea (Atka Bay, Kapp Norvegia), Antarctica

east side, it was separated according to depth, from deep to shallow, into three distinct transects; after a certain distance without video observation, the fourth part of this transect (ANT XIII, stn 24II) was situated on the south-west slope of the bank at around 120 m depth. One additional transect was videotaped on this slope between 60 and 90 m (ANT XVII, Stn 111-1).

In the second study area, northern Marguerite Bay off the west coast of the Antarctic Peninsula (Fig. 1), video transects were carried out by the British Antarctic Survey research vessel R.R.S. “James Clark Ross” (cruise JR37). The land, as well as the seascape, and, consequently, the coastline, are quite variable and heterogeneously structured here. The transects covered depths

<57 m. The 160-m-depth contour was defined as the lower depth limit for this study at all three sites.

Faunal analysis

All organisms >1 cm were counted and identified to the lowest possible taxonomic level at the given optical resolution of the cameras. Organisms were identified based on literature (Thomson and Murray 1880 to 1889; Discovery Committee Colonial Office 1929 to 1980; Sieg and Wägele 1990) and on experts, who identified original material from the study sites and also assisted in the identification of different taxa (see "Acknowledgements"). Most of these specialists contributed to a comprehensive species list for the Weddell Sea (Gutt et al. 2000). Imaging methods, however, arise some problems: (1) in some cases individuals cannot be distinguished from other organisms, especially where sponges, hydrozoans, and bryozoans nearly fully cover the sea bottom, and (2) density estimates are influenced by optical resolution and, thus, limited species identification. Colonies of colonial taxa were counted and treated as single individuals in the statistical analyses. Where this approach proved impossible, because of the irregular shape of the colony, percentage cover of the sea-floor was determined and used as a proxy for true abundances. Abundances were standardised to numbers per 100 m^2. In order to facilitate identification of the organisms, an average of 100 still photographs was also taken by the ROV at each station along the same transects and consulted in addition to the videos.

Data analyses

Multivariate analyses were based on a matrix containing standardised abundances for each station. Taxa with an overall relative abundance of <4% were eliminated, as suggested by Field et al. (1982), in order to exclude bias of the results due to rare taxa. Fourth-root transformation

was used to reduce the contribution from numerically dominant species and to reveal changes among less dominant species (Field et al. 1982). Similarities between stations and taxa were calculated using the Bray-Curtis coefficient. Nonmetric multidimensional scaling (MDS) was employed for ordination. This method plots complex multivariate relationships in two dimensions. A low (<0.2) MDS stress coefficient indicates that the multivariate similarity pattern is represented by the plot without much distortion (Clarke 1993). Significance tests for differences among sites were carried out using one-way ANOSIM (analysis of similarities, a multivariate analogue of ANOVA, Clarke and Green 1988) permutation tests. The *R*-statistic gives an absolute measure of the degree of discrimination between all sites or pairs, on a scale of 0-1, representing a range from indistinguishable to perfect discrimination. The nature of the community groupings identified in the MDS ordination was explored further by using the similarity percentages (SIMPER) routine to determine the contribution of individual taxa to the average dissimilarity between samples (Clarke 1993). The majority of the techniques are described in Clarke and Warwick (1994) and were implemented using PRIMERv5 (Plymouth Routines in Multivariate Ecological Research; Clarke and Gorley 2001).

Results

Number of taxa

A total of 237 taxa were identified comprising of 85,538 individuals: 50 taxa of sponges, 57 cnidarians, 1 nemertean, 1 echiurid, 9 molluscs, 17 polychaetes, 2 pycnogonids, 4 crustaceans, 2 hemichordates, 26 ascidians, 38 echinoderms, 22 bryozoans and 8 fish. The number of taxa per station ranged between 58 and 115 (Table 1).

Community analysis

The MDS ordination revealed three distinct groups (Fig. 2) corresponding to the three studied sites: Marguerite Bay (Antarctic Peninsula), Atka Bay and Four Seasons Bank in the Weddell Sea. For this ordination, the stress was considered to be good (0.11), with no real risk of drawing false inferences. A clear depth gradient was determined for Four Seasons Bank, where the shallow station (24II-S) was separated from the middle-depth stations (111-1, 24II-M) and the deepest stations (24II-D, 24II-B). The use of ANOSIM confirmed that the groups obtained were significantly different (P<0.001) from each other, since the global R-value of 0.915 was higher than the threshold value of 0.15 (the value delivered by the null-hypothesis that there is no difference between samples). R-statistic values for pairwise comparisons lying near 1 demonstrated significant difference also between groups, since significant levels for all pairs were clearly <5% (Table 2).

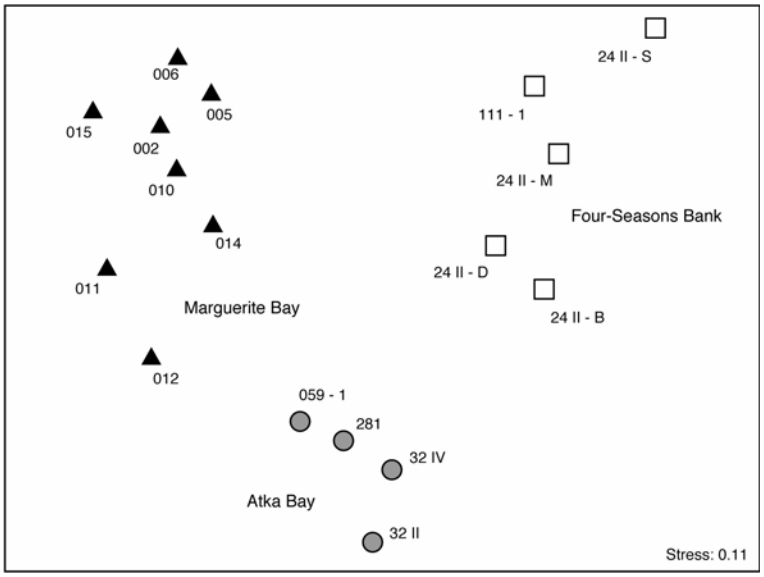

Fig. 2 Nonmetric multidimensional scaling ordination based on Bray-Curtis similarity derived from fourth-root-transformed abundance data. *Symbols* represent groupings of stations according to cluster analysis (*S* shallow; *M* middle; *D* deep: *B* fourth part of the transect on the south-west slope)

Table 1 Study sites. Water depth average (ranges in *parentheses*), mean total number of taxa per station and abundance (n/100m^2) of the 60 most-dominant taxa in the entire dataset. [*ASC* Ascidiacea; *AST* Asteroidea; *BRY* Bryozoa; *COR* Hexacorallia; *DEM* Demospongiae; *ECH* Echinodermata; *GOR* Gorgonacea; *HEX* Hexactinellida; *HOL* Holothuroidea; *HYD* Hydrozoa; *OCT* Octocorallia; *POL* Polychaeta; *S* shallow; *M* middle; *D* deep; *B* fourth part of the transect at the south-west slope; *asterisk* indicates *Rosella racovitzae* (budding type)]

	Marguerite Bay								**Atka Bay**				**Four Seasons Bank**				
No. Stations	8								4				5				
Depth (m)	94 (57-158)								112 (62-139)				97 (55-147)				
Taxa (total)	71 (62-88)								92 (78-115)				78 (58-92)				
Stations	**002**	**005**	**006**	**010**	**011**	**012**	**014**	**015**	**059-1**	**281**	**32II**	**32IV**	**111-1**	**24II-S**	**24II-M**	**24II-D**	**24II-B**
Species																	
Rosella racovitzae (HEX)	26.6	36.7	0.0	0.6	10.8	0.0	1.6	1.4	51.8	3.0	33.4	55.0	1.8	0.0	0.0	0.0	8.6
*Rosella racovitzae** (HEX)	751.2	2730.0	2444.2	188.9	0.0	6.0	0.0	972.6	1.0	0.0	3.3	31.7	0.0	0.0	0.0	0.0	9.7
Scolymastra joubini (HEX)	3.5	1.1	0.0	0.0	2.5	0.0	7.8	0.7	503.9	4.0	34.8	42.1	0.9	3.2	1.0	12.2	23.7
Cinchyra antartica (DEM)	11.6	4.5	5.7	4.2	4.2	0.0	0.5	1.4	12.3	1.5	5.7	53.4	4.4	0.0	0.5	1.7	5.9
Cinchyra barbata (DEM)	13.9	3.4	4.3	2.3	0.0	0.5	1.6	2.2	5.6	0.0	3.5	56.5	69.4	5.7	58.2	232.1	1557.5
Haliclonidae spp. (DEM)	4.6	0.6	0.0	0.6	1.7	3.8	16.1	1.4	2.1	2.0	3.3	7.9	17.6	10.9	107.0	175.4	0.5
Haliclona sp. (DEM)	4.6	4.0	3.5	0.0	0.0	0.5	0.0	2.9	0.0	0.0	0.0	0.0	7.3	0.0	0.5	2.8	348.0
Homaxinella spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	72.6	149.4	297.7	1.7	0.0
Iophon radiatus (DEM)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	9.2	0.0	51.9	11.4	2.6	0.0	3.4	4.4	71.8
Monosyringa longispina (DEM)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	13.5	69.2	24.4	0.0	0.0	0.0	0.6	46.4
Stylocordyla borealis, oblong (DEM)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	0.5	0.0	2.4	0.0	2.6	71.5	50.8	11.7	27.5
Stylocordyla borealis, round (DEM)	6.9	1.7	1.4	1.7	2.5	23.3	7.8	3.6	0.5	5.5	28.1	2.0	6.2	0.0	10.3	86.6	7.7
Tedania tantula (DEM)	0.0	9.4	5.7	4.2	2.5	0.0	1.6	0.0	7.2	8.0	9.5	4.5	0.0	0.0	106.6	188.8	52.9
Tetilla leptoderma(DEM)	1.2	4.5	5.7	63.2	2.5	11.4	1.6	0.7	15.9	2.5	1.5	25.3	1.8	0.8	1.5	3.3	0.5
Demospongiae spp.	113.2	155.4	103.6	45.9	20.9	26.6	14.6	59.2	44.1	27.0	32.5	86.3	145.9	79.1	56.2	34.4	23.2
Demospongiae sp.13	46.2	0.6	2.1	6.9	5.8	0.0	1.4	12.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
“Fan shape” (DEM)	1.2	2.3	3.5	1.1	21.7	1.3	2.9	2.2	0.5	133.4	0.5	3.0	0.0	0.0	8.3	7.2	2.7
“Yellow branches” (DEM)	4.6	22.7	104.3	28.1	0.0	0.0	89.5	0.0	171.2	0.0	78.6	34.3	1.8	0.0	1.0	121.0	0.0
Hydrozoa spp.	120.2	40.7	55.3	64.9	78.5	274.1	48.9	55.6	380.8	265.8	139.2	138.3	213.5	16.1	37.1	44.4	62.0
Hydrozoa sp.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	254.0	0.0	0.0	18.9	0.5
Corymorpha parvula (HYD)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	55.9	1.0	0.5	121.5	185.4	11.7	0.0	3.3	1.8
Corymorpha sp.1 (HYD)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	0.5	0.0	0.0	257.5	0.0	0.0	0.0	0.0
Oswaldella antarctica (HYD)	0.0	0.0	0.0	0.0	0.0	0.5	34.3	0.0	0.0	175.4	3.3	0.5	37.6	337.5	179.9	182.7	17.8
Schizotricha cf. *unifurcata* (HYD)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	54.5	213.6	478.5	24.4	43.7
Symplectoscyphus spp. (HYD)	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	19.0	0.0	0.0	0.0	0.9	66.6	33.2	12.2	0.0
Tubularia ralphii (HYD)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8938.6	5.9	0.0	59.9
Clavularia cf. *frankliniana* (OCT)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	283.0	1052.5	151.0	0.6	0.0
Arntzia sp. (GOR)	0.0	2.3	1.4	0.6	0.0	0.0	6.2	0.0	0.0	3.5	0.0	0.0	97.5	416.2	1406.3	184.9	9.2
Dasystenella spp. (GOR)	9.2	0.0	0.0	4.6	0.0	28.8	2.6	5.6	2.1	6.0	3.3	1.0	4.4	0.0	2.0	16.7	0.0
Fanyella spp. (GOR)	0.0	1.7	2.8	2.9	0.0	2.2	0.0	0.	13.8	56.5	0.0	0.0	35.1	3.2	0.0	0.6	1.6

Table 1 [continued] Study sites. Water depth average (ranges in *parentheses*), mean total number of taxa per station and abundance (n/100m^2) of the 60 most-dominant taxa in the entire dataset. [*ASC* Ascidiacea; *AST* Asteroidea; *BRY* Bryozoa; *COR* Hexacorallia; *DEM* Demospongiae; *ECH* Echinodermata; *GOR* Gorgonacea; *HEX* Hexactinellida; *HOL* Holothuroidea; *HYD* Hydrozoa; *OCT* Octocorallia; *POL* Polychaeta; *S* shallow; *M* middle; *D* deep; *B* fourth part of the transect at the south-west slope; *asterisk* indicates *Rosella racovitzae* (budding type)]

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Species																	
Primnoella sp.1 (GOR)	79.7	14.7	15.6	102.8	12.5	5.4	50.5	115.6	0.5	5.0	0.0	0.5	65.9	26.6	85.5	9.4	32.4
Primnoella sp.2 (GOR)	11.6	102.3	132.7	57.4	1.7	15.3	9.9	1.4	0.5	5.0	0.0	0.0	23.7	2.4	20.0	89.9	0.5
Primnoisis spp. (GOR)	4.4	0.0	1.4	8.6	3.3	45.6	2.9	19.6	17.9	8.5	21.9	5.9	0.0	1.2	159.8	159.3	127.3
Thouarella spp. (GOR)	19.6	6.8	1.4	28.1	20.0	124.3	47.3	19.6	45.1	95.4	5.7	19.3	1.5	0.0	97.3	206.5	9.7
Actinaria sp.20 (COR)	83.2	0.0	0.0	0.0	0.0	0.0	0.0	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ceriantharia spp. (COR)	69.3	1.7	13.5	13.3	50.9	1.9	2.3	2.2	8.7	1.0	0.0	0.0	6.2	4.0	0.0	5.6	0.0
Ceriantharia sp.5 (COR)	16.2	0.6	0.0	0.0	0.0	0.0	0.0	57.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Melicerita obliqua (BRY)	0.0	0.0	0.0	0.0	0.8	2.2	0.0	0.0	488.5	236.8	3863.8	274.1	0.0	0.0	0.0	0.6	0.0
Sabellidae spp. (POL)	0.0	5.7	5.7	2.3	9.2	356.6	11.4	0.0	10.8	0.0	4.8	5.5	21.1	5.2	83.1	83.3	1.1
Sabellidae sp.5.(POL)	34.7	0.0	1.4	0.0	1.7	2.2	27.1	3.6	14.9	147.4	2.9	0.0	78.2	0.0	0.0	0.0	148.4
Sabellidae sp.7 (POL)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	192.7	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Polychaeta sedentaria spp.	0.0	1.7	7.1	7.5	9.2	0.0	71.3	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0
Polychaeta sedentaria sp.1	1.4	0.0	0.0	4.2	15.0	917.6	2.6	6.5	1.5	1.5	1.4	0.0	89.6	101.3	100.7	20.5	3.2
Pycnogonida spp.	0.0	0.0	0.0	1.1	0.0	2.7	0.5	0.0	4.1	1.5	0.5	1.0	66.8	39.2	18.6	7.2	8.9
Asteroidea spp.	18.5	18.9	13.5	8.6	3.3	21.2	17.2	2.9	20.0	11.5	5.2	5.5	3.8	11.3	7.3	25.5	5.4
Macroptyaster spp. (AST)	4.6	11.9	20.6	4.2	2.5	4.3	6.8	2.2	1.0	0.5	0.5	3.5	5.3	1.2	1.5	0.6	1.8
Ophiuroidea spp.	3923.7	3856.4	4574.8	3766.4	923.1	657.3	2589.2	2464.6	593.6	92.4	291.7	136.8	174.0	35.5	88.0	184.9	243.8
Sterechinus neumayeri (ECH)	1653.4	1656.7	1857.5	884.2	32.5	29.3	54.7	654.7	26.1	1.0	0.5	0.0	488.6	2943.1	101.2	26.6	34.5
Dendrochirotida (HOL)	2.3	0.6	1.4	1.7	10.0	34.2	214.9	1.4	217.8	38.5	27.6	5.7	12.3	184.5	25.9	12.2	1.8
Ekmocucumis turqueti (HOL)	16.2	0.6	0.7	0.0	0.0	0.5	9.9	2.9	94.8	38.5	8.7	8.9	1.2	17.8	21.5	2.2	3.2
Crinoidea spp.	5.8	0.0	0.0	0.0	3.3	638.9	5.2	0.7	54.3	39.5	86.3	37.7	0.9	0.8	23.5	33.3	2.2
Cnemidocarpa verrucosa (ASC)	9.2	44.7	51.1	1.7	6.7	0.0	5.5	5.6	10.3	1.0	0.0	0.5	0.9	0.8	0.0	0.6	1.8
Molgula peduncolata (ASC)	42.7	6.8	18.4	1.7	4.2	14.7	6.2	34.7	6.2	3.0	0.0	2.5	0.9	0.0	0.5	0.0	2.2
Pyura discoveryi (ASC)	67.1	0.0	38.3	7.5	0.0	2.7	1.4	2.2	4.6	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0
Aplidium sp.3 (ASC)	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	16.4	3.0	11.4	136.3	0.9	0.0	1.0	2.2	2.2
Polycitoridae sp.2 (ASC)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.9	343.3	6.2	2.0	0.0	0.0	0.0	1.7	0.0
Polyclinidae spp.(ASC)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	89.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scycozoa sp. 1 (ASC)	22.0	7.3	0.0	12.6	3.3	8.7	12.0	2.2	4.1	0.0	1.0	0.5	1.8	0.0	0.0	0.0	0.0
Synoicum adareanum (ASC)	0.0	0.0	2.1	0.0	0.0	0.0	0.0	0.0	35.4	6.0	417.7	469.9	0.0	0.0	0.0	6.1	8.6
Synascidiacea sp.32 (ASC)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.2	16.0	17.6	18.8	0.0	8.5	3.9	1.1	0.0

Table 2 Results of one-way ANOSIM randomisation test based on similarity measures derived from macrofaunal abundance estimates, examining differences in the structure of the assemblages at each location, Global *R*=0.915 (P<0.001) (*MB* Marguerite Bay; *AB* Atka Bay; *FS* Four Seasons Bank)

Groups	*R*-statistic	Significance Level %	Possible Permutations
MB, AB	0.886	0.2	495
MB, FS	0.958	0.1	1287
AB, FS	0.888	0.8	126

Faunal composition

In Marguerite Bay Ophiuroidea spp. were most abundant, followed by the hexactinellid sponge *Rossella racovitzae* (budding type; according to Barthel and Gutt 1992), the regular sea urchin *Sterechinus neumayeri*, a sedentary polychaete species, and hydrozoans (Table 1). Only two species, *R. racovitzae* and *S. neumayeri*, served as good key species. The latter also reached relatively high average abundances at the other sites; however, in Marguerite Bay, it was most homogenously distributed over the stations, indicated by a high δi/SD(δi) value (Table 3).

The stations in and close to Atka Bay were dominated by the bryozoan *Melicerita obliqua*, Ophiuroidea spp. and the compound ascidean *Synoicum adareanum*. The phylum Porifera was represented with a high abundance of the glass-sponge *Scolymastra joubini* at a single station (059-1) (Table 1), but this species was very rare at the shallowest station in the inner part of Atka Bay. The analysis of key species identified *M. obliqua*, *S. adareanum* and the demosponge *Monosyringa longispina* as being typical for the fauna at this site (Table 3).

Table 3 Characteristic species for each group of stations, as determined by similarity percentage (SIMPER) analyses based on fourth-root-transformed abundance data and the Bray-Curtis measure of dissimilarity [δ and δ_i the overall dissimilarity and individual contribution to the average dissimilarity, respectively, between groups; *SD*(δ_i) standard deviation; *MB* Marguerite Bay; *AB* Atka Bay; *FS* Four Seasons Bank; *OS* others; asterisk indicates *Rosella racovitzae* (budding type)]

Group	Taxa	Average Abundance				Average Term δi	δi/SD(δi)
		MB	AB	FS	OS		
MB vs OS	*Rosella racovitzae* *	886.61			5.08	1.35	1.39
δ=56.71	*Sterechinus neumayeri*	852.88			402.40	1.12	1.48
	Oswaldella antarctica	4.35			103.86	0.88	1.54
AB vs OS	*Melicerita obliqua*		1215.80		0.28	1.84	2.52
δ=54.72	*Synoicum adareanum*		232.25		1.29	1.12	1.83
	Monosyringa longispina		27.03		3.62	0.71	2.08
FS vs OS	*Arntzia* sp.			422.82	1.17	1.27	1.96
δ=56.67	*Schizotricha* cf. *unifurcata*			162.94	0.00	1.23	2.98
	Oswaldella antarctica			151.10	17.83	0.99	1.94
	Clavularia cf. *frankliniana*			297.42	0.00	1.08	1.28
	Tubularia ralphii			1800.88	0.00	1.13	0.76

The hydroid *Tubularia ralphii*, the sea urchin *S. neumayeri* and the gorgonian *Arntzia* sp. were the most dominant taxa at the Four Seasons Bank. The demosponge *Cinachyra barbata* was also abundant at this site (Table 1). The characteristic taxa for this site were *Arntzia* sp., and the hydroids *Schizotricha* cf. *unifurcata* and *Oswaldella antarctica*. Furthermore, the sponge *Homaxinella* spp. was abundant at this site (Table 1), with number of individuals between 2 and 298 per 100 m^2. In this study the hydroid *T. ralphii* and the octocoral *Clavularia* cf. *frankliniana* were found only at the Four Seasons Bank. However, they did not show high values of dissimilarity (δi) because they were patchily distributed with high abundances only at the shallow transects of stn 24II, which is indicated by the relatively low δi/SD(δi) value (Table 3). Consequently, they can also be considered typical for this group of stations, but their role as key species is only moderate.

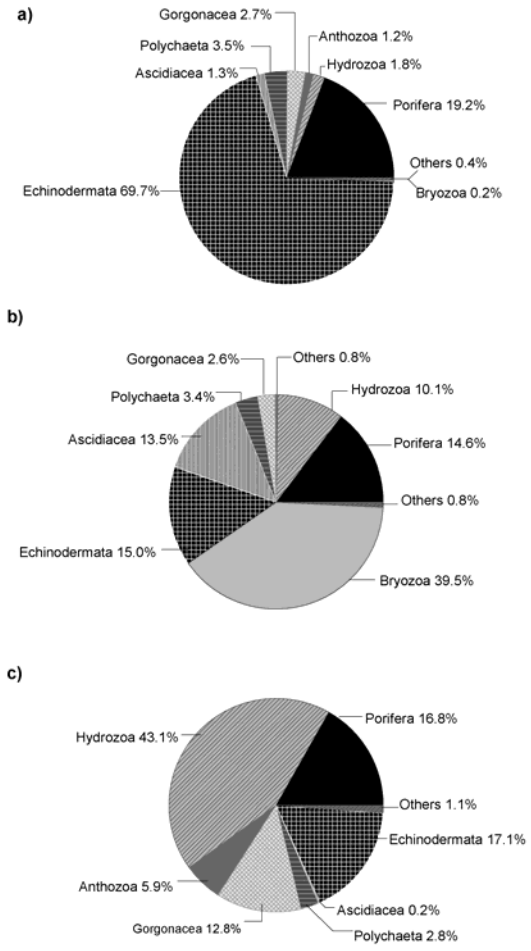

Fig. 3 Abundance (%) of major taxonomic components in the station clusters distinguished in the study area: **a** Marguerite Bay, **b** Atka Bay, **c** Four Seasons Bank

Furthermore, on a coarse taxonomic level, the faunal composition appeared to be different between the three study sites (Fig. 3). The echinoderms (69.7%), and particularly ophiuroids, dominate the fauna in Marguerite Bay. At Atka Bay bryozoans had the highest proportion (39.5%), and ascidians (13.5%) were well represented. At Four Seasons Bank hydroids were the most dominant (43.1%) and, in this group, in contrast to the other sites, gorgonians (12.8%) were more important. Sponges and polychaetes were more evenly distributed across the three different sites.

Discussion and conclusions

The general aim of this study was to compare benthic community composition at three different sites, to determine whether this composition was influenced more by long-distance dispersal and

local environmental conditions, or by colonisation from nearby deeper water. Three study sites shallower than 160 m were sampled. The Atka Bay and Four Seasons Bank transects are both situated in an area where hydrodynamics are dominated by the westward coastal current (Fahrbach et al. 1992), which is part of the large clockwise Weddell Gyre. The benthic community in adjacent deeper waters is rich and relatively homogenous (Voß 1988; Gutt and Starmans 1998; Gutt and Schickan 1998; Starmans et al. 1999; Starmans and Gutt 2002). The third station, in northern Marguerite Bay, west of the Antarctic Peninsula, has by far the highest proportion of a true coast with adjacent shallow waters (Kennedy and Anderson 1989; Bonn et al. 1996), influenced by a prevailing westward current along the coast (Hofmann et al. 1996).

The community analyses revealed significant differences between the fauna of all three sites. The faunistic distances between sites and the degree of homogeneity within the sites were similar, with the exception of a more homogenous pattern at Atka Bay, which might be because only four stations were analysed at this site. *First main conclusion:* there is no homogenous shallow-water benthos between 60 and 160 m depth; instead, different assemblages were found independent of their geographical location.

The next question is whether the faunistic differences reflect the spatial distances between the study sites. Since there are few shallow-water areas to act as stepping stones, colonisation of isolated areas of shallow water could be dispersal limited (Clarke 1996b). The *R*-statistic values representing faunistic similarities between all sites are similar to each other, with a slightly higher distance between Marguerite Bay and Four Seasons Bank, which is also shown in the MDS plot. Geographical distances, which represent, at least theoretically, routes of dispersion, differ considerably from this pattern. Atka Bay and Four Seasons Bank are in relatively close

proximity, since they are not >330 km apart. If distances in space play a dominant role in explaining benthic structures, some of the most abundant species at the Four Seasons Bank would also be expected at Atka Bay, because they could be dispersed by the westerly current. Although a depth gradient was found within the data from Four Seasons Bank, differences between all sites were significant. For an exchange of fauna between the two sites in the eastern Weddell Sea and the area west of the Antarctic Peninsula, two different routes can be assumed. The first would start in Marguerite Bay, cyclonically following the Eastwind Drift and travelling three-quarters of the entire continent of approximately 11,000 km before arriving the Weddell Sea. From here dispersion could follow the Weddell Gyre and enter the Bransfield Strait from the region off Joinville Island at the tip of the Antarctic Peninsula (Gordon et al. 2000) leading back to the Marguerite Bay. The second route would be dispersal via the Westwind Drift, clockwise from Marguerite Bay. Even by this route, however, the distance to the eastern coast of the Weddell Sea would be ten times longer than the distance between the two sites in the Weddell Sea. *Second main conclusion:* benthic assemblages in Antarctica are not shaped significantly by the limitation of long-distance dispersion, because of the existence of few shallow-water areas not being covered by the ice shelf.

Although information on generality in reproduction strategies and early life history is scarce, it seems worthwhile to check some species dominant at our sites for common characteristics regarding the potential to disperse. Several abundant Antarctic invertebrates are short-distance dispersers, either because they reproduce asexually or because they brood their juveniles (Arntz et al. 1994). These reproductive strategies support the local success of single species (Bolker and Pacala), and, if these species become dominant, the community structure can be shaped considerably. Asexual reproduction via budding is prevalent, e.g. in the hexactinellid sponge

Rosella racovitzae (budding type; according to Barthel and Gutt 1992), and brooding seems to be a common feature of reproduction in Antarctic octocorals, e.g. gorgonians (Orejas et al. 2002). The stoloniferous coral *Clavularia* cf. *frankliniana* broods its embryos, and asexual propagation via fission is common (Slattery and McClintock 1997). Long-range dispersion among sessile animals by pelagic planktotrophic larvae, e.g. *Sterechinus neumayeri* and other abundant invertebrates (Bosch et al. 1987, Pearse et al. 1991), supports the coexistence of many species, as has been shown by a spatially explicit model (Potthoff, Johst, Gutt, Wissel unpublished results), and leads to a high capacity to colonise highly disturbed habitats (Poulin et al. 2002). The marked differences in the reproductive mode of some dominant species within a single site might be an additional reason for the faunistic differences between sites.

In order to confirm a certain generality of our results, some species typical or abundant at our sites were checked for their circumpolar distribution: *R. racovitzae, Scolymastra joubini, Cinachyra barbata, Monosyringa longispina* (Koltun 1969; Sarà et al. 1992; Gutt and Koltun 1995), and *Synoicum adareanum* (Kott 1969) all have a clear circumpolar distribution and cover a broad depth range. A species reported as common in widely separated areas, but with less evidence of a widespread circumpolar distribution than those mentioned above is *S. neumayeri*, present along the Antarctic Peninsula, Weddell, Ross and Davis Seas (Pawson 1969). The reason for this might be related to the obvious preference of waters shallower than 300 m (Brey and Gutt 1991). Indeed at Syowa research station, Hamada et al. (1986) described differences in faunal composition at different depths and noted the lack of *S. neumayeri* at 200 m, where bryozoans were very dominant. The hydroid *Tubularia ralphii* has an even more obvious preference for shallow water and, so far, has only been found above 36 m water depth around Antarctica (Dayton et al. 1970, 1974; Propp 1970; Gruzov 1977; Stepaniants 1980; Barnes and Bullogh

1996), although in our study it reached a maximum depth of 104 m at Four Seasons Bank. A similar pattern was shown by the octocoral *Clavularia* cf. *frankliniana*, which is known from the Weddell Sea (present study), South Georgia (Molander 1929) and McMurdo Sound (Dayton et al. 1970, 1974; Slattery and McClintock 1995, 1997), where it is "numerically dominant" between 12 and 33 m and seems to be a true shallow-water taxon. The new gorgonian genus *Arntzia* belongs to those taxa that obviously prefer deeper waters, since their shallowest occurrence has been recorded in the Weddell Sea (64 m) and it is known from the Scotia Arc and the Weddell and Ross Seas, but not from other sites in East Antarctica (López-González et al. 2002). Two species that seem to have a limited distribution on the continental shelf are *Oswaldella antarctica*, found at the Antarctic Peninsula (Peña Cantero and Vervoort 1998) and at Four Seasons Bank (present study), and *Schizotricha* cf. *unifurcata*, recorded mainly from sub-Antarctic islands in the Indo-Pacific sector of the Antarctic, as well as in the Weddell Sea (Peña Cantero 1998). *Third main conclusion:* each of the shallow-water assemblages examined in this study has a specific faunal composition, but there is no indication for a generally unique fauna at any of these sites due to a mixture of species with circumpolar and more specific distributions.

Another reason for the specific faunistic compositions at the three sites could be the considerable exchange with deeper assemblages. In a critical short review of the frequently described "eurybathy" among Antarctic invertebrates, Gutt (1991) suggests that assemblages may also be eurybathic between 160 and 1,180 m. The complete eurybathy of the Weddell Sea benthos was demonstrated by Brey et al. (1996); however, at that time, the shallow sites were not yet known or had not been investigated, and species that occurred elsewhere in shallow waters were ignored, which reduces the representativity of the results. Use of the 160-m-depth contour as the lower limitation in the present study does not coincide with any clear benthic depth zonation; the depth

limitation ensures only that the presence of species restricted to shallow waters is likely to be detected and that assemblages typical of deeper waters are partly represented. Some examples of abundant and typical species have already been discussed. In addition, Hamada et al. (1986) described differences in faunal composition at different depths and noted the lack of *S. neumayeri* at 200 m, where bryozoans were very dominant. Cattaneo-Vietti et al. (1997) mentioned the presence of large beds of *Adamussium colbecki* up to 70-80 m depth, which are abundant, but patchily distributed. Furthermore, Cattaneo-Vietti et al. (2000) indicated that the bivalves *A. colbecki* and *Yoldia eightsi* seemed to be restricted to shallow water (200 m) at Terra Nova Bay. If the exchange between deeper and shallower benthos is important, then the two sites in the Weddell Sea should be, by far, more similar to each other than is either to the Marguerite Bay site, because they are located in an area, where just one quite homogenous community exists on the deeper shelf (Gutt 2000). However they are not. *Fourth main conclusion:* the Antarctic shallow-water benthos is not shaped by intensive exchange with the deeper fauna, although it is not isolated from these assemblages.

We came to the conclusion that shallow-water benthic assemblages in the Antarctic are shaped mainly by local environmental conditions rather than by specific large-scale processes. Clarke (1996a), identified a number of factors including depth, habitat, bottom topography and oceanography as those with the most effective influence on benthic distribution. In relation to our scientific question, Antarctic benthic assemblages are affected by the ability of species to disperse around Antarctica and the physical stresses delimiting general patterns of distribution and abundance (where the latter refers to locally specific and not only to circumpolar conditions such as the permanently low temperatures). In this context, an interesting taxon is the sponge genus *Homaxinella*, of which *H. balfourensis* is abundant and *H. flagelliformis* is known only

from the Magellan region (excluding the Falkland Islands), Kerguelen Islands (Sarà et al. 1992), and the Ross and Lazarev Seas (Pansini et al. 1994; Gutt and Koltun 1995). All known habitats of this genus are related to quite specific, small-scale areas that have recently been disturbed by glaciers, icebergs, or anchor ice (Dayton 1989; Dawber and Powell 1997; Gutt 2000). Both species also occur in the Weddell Sea, and at least one of them is extremely abundant where iceberg scouring is frequent, especially at Four Seasons Bank (298 individuals per $100m^2$ at stn 24II). Clearly, these species have the potential to disperse around the Antarctic continent, using disturbed areas with their associated specific environmental conditions as stepping stones; however, such species are probably displaced by competitive exclusion as succession proceeds and consequently are very rare in undisturbed areas (Dayton 1989). This may apply to both species, of which *H. balfourensis* seems to be less and *H. flagelliformis* more selective, in terms of environmental demands. A similar case is the deep occurrence of *Tubularia ralphii*, which lives elsewhere in the Antarctic, in a depth zone that is regularly but not very frequently disturbed by sea-ice (Dayton et al. 1970, 1974; Propp 1970; Gruzov 1977; Barnes and Bullogh 1996) and which, obviously, at its lower depth limit in the Weddell Sea, is affected by icebergs. In general, Four Seasons Bank seems to support special faunal assemblages of organisms that are not very common in other benthic Antarctic areas. This could be influenced by special environmental conditions originating as a result of the topography of the bank. Strong currents and generally enhanced variability above the banks have been observed frequently (Genin et al. 1986; Beckmann 1999). Hydroids and anthozoans, especially gorgonians, were well represented in these station groups. Strong currents are an advantage for the establishment of this group of organisms, because currents supply them with food and continuously keep the substratum and the organisms completely clear of sediment (Genin et al. 1986, Rogers 1994).

As previously mentioned, it is remarkable that the difference between the faunas of the neighbouring areas, Atka Bay and Four Seasons Bank, is almost as great as that between these areas and the western Antarctic Peninsula. We discussed the possibility that specific environmental conditions may dictate differences at the community level. However, additional mechanisms exist that might contribute to the benthic structure; one of these is the very limited dispersal and associated gene flow which may promote genetic and morphological differences at a scale of just a few kilometres (Wägele, 1992; Poulin and Féral 1994; Allcock et al. 1997). The observed overlap of species' presences in different assemblages, in combination with genetic differences, could also be the result of re-establishment on the high-Antarctic shelf following the most recent glacial maximum, after which many parts of the shelf became available again for the benthos (Harris and O'Brien 1996). In this phase (approximately the last 5,000 years: Dayton and Oliver 1977) genetic differentiation in a relatively stable environment is only the first step towards speciation and the occupation of different ecological niches (Grassle and Sanders 1973), a phenomenon known as "vicariance" or "climate diversity pump" (Clarke and Crame 1997). Different substratum types (e.g. hard substrata, sandy areas, living organisms used as substratum, or biogenic structures, such as mats of sponge spicules), the presence of specific current regimes and a variety of bottom topographies influencing the food supply for filter feeders, together with a reduced ability to disperse, have provided the opportunity for some populations to develop uniquely. It is therefore only a matter of time until endemic species will occur in specific Antarctic benthic habitats, and, consequently, the number of Antarctic invertebrate species will increase. Recently, in some groups (for example crustaceans and bivalves: Held 2003; Katrin Linse pers. comm.), closely related "cryptic" species have been found, indicating that speciation processes remain active in Antarctica (Clarke and Crame 1997).

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Publication II

Antarctic mega-epibenthos: horizontal seriation and depth zonation by examples

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Abstract

Spatial patterns of Antarctic benthic shelf communities were studied using underwater video. Examples of patterns of "seriation" found in the shallow-water mega-epibenthic fauna in the Marguerite Bay (Adelaide Island, Bellingshausen Sea) and the Weddell Sea are given. For horizontal seriation a total of 12 seabed video-strips were conducted at 9 stations between 55 and 160 m. The index of multivariate seriation (IMS) showed eight significant results for horizontal seriation. Stations with non-significant seriation values belong to those with the smallest range of species or faunal-heterogeneity but with intermediate values for species turnover (median of Bray-Curtis values). Conversely stations with relatively good faunal seriation displayed broad ranges of species turnover. Depth zonation (60-143 m) was observed and analysed at Four Seasons Bank (Weddell Sea). This bank seems to comprise several faunal assemblages which combines a clear depth gradient and a zonation with discrete assemblages. Results show that different patterns are identifiable: a locally limited typical fauna, a patchwork of assemblages as well as continuous faunistic gradients. Combinations of these three scenarios can be considered as the rule in Antarctic mega-epibenthic communities.

Key words: Mega-epibenthos, Antarctic, seriation, depth zonation, multivariate analyses, IMS, underwater video, ROV

Introduction

Research on patterns and processes in benthic communities of the Southern Ocean is of general interest to characterize their structure, to describe their function and to understand their development (White 1984, Arntz et al. 1994, Clarke 1996c). Zonation might be defined as a familiar and ubiquitous organisation of organisms by geography, topography and exposure (Barnes and Brockington 2003). Clear-cut zonation patterns in the form of a serial change in community structure with increasing water depth are a striking feature of intertidal and shallow-water benthic communities on both hard and soft substrata (Clarke and Warwick 1994).

Zonation is a common benthic distribution feature of continental slopes (Carey and Ruff 1977, Dayton 1994) and has been a research topic at different latitudes (Rowe and Menzies, 1969, Dayton et al. 1970, Carey et al. 1975, Abbiati et al. 1987, Hecker 1990, Simboura et al. 1995, Piepenburg and Schmid 1996, Cattaneo-Vietti et al. 2000a). Possible causes of zonation patterns are diverse, and may vary according to environmental conditions and ecological demands of assemblages with their specific species composition.

The benthos of the Southern Ocean is influenced by a number of factors including depth, currents, sediments, bottom topography, light or wave energy, ice scouring, competition and predation (Dayton et al. 1974, Dayton 1989, Arntz et al. 1994, Clarke 1996a, 1996c, Slattery and Bockus 1997, Stanwell-Smith and Barnes 1997, Gutt 2000). None of these mechanisms, however, will necessarily give rise to discontinuous bands of different assemblages of species, which is implied by the term “zonation”. Therefore, the more general term “seriation” (zonation with no sharp discontinuities) is perhaps more appropriate to describe continua of changing

communities (Clarke et al. 1993, Gherardi and Bosence 2001, Brown et al. 2002). The present study describes examples of patterns of "seriation" found in the shallow-water mega-epibenthic fauna in the Marguerite Bay (Adelaide Island, Bellingshausen Sea) and the Weddell Sea, independently of the existence of a depth gradient.

Many shallow inshore waters of the Antarctic coastal zone are poorly sampled (Arntz et al. 1994) and corresponding hard-bottom biotopes are poorly known also because these are not easily accessible (Gambi et al. 2000a). The mega-epibenthos in the Bellingshausen Sea has been until now not intensively studied. Recent descriptions of the fauna of the Marguerite Bay indicate the lack of the dominance of sponges and bryozoans in the mega-epibenthic assemblages (Starmans et al. 1999). A zonation pattern for littoral areas was proposed by Barnes and Brockington (2003), and Barnes and Arnold (2001) describe polar boulder shore assemblages with fewer species and considerably less variability compared with those at other latitudes. Zonation at hard (0.5–60 m) (Dayton et al. 1970, Gruzov and Pushkin 1970, Propp 1970, Gruzov 1977, Gambi et al. 1994, 2000a), soft (0-25 m) (Nonato et al. 2000) and mixed (0-150 m) (Zamorano 1983, Kirkwood and Burton 1988, Cattaneo-Vietti et al. 2000a) bottoms in the Antarctic has been described and diverse zonation schemes for these biotopes have been proposed.

The aims of the present investigation were: (1) to study for the first time horizontal seriation of mega-epibenthic assemblages by underwater video at intermediately shallow water depth (53 to 143 m) with a mixture of hard and soft bottoms in different Antarctic regions, (2) to analyse simultaneously horizontal seriation and vertical zonation, especially in this depth stratum in the Weddell Sea where both phenomena can not only be expected but where corresponding areas are

also accessible to sampling activities and (3) to identify environmental conditions which can either lead to clear zonation and/or seriation or which, alternatively, superimpose these, resulting in an obvious pattern variability.

Material and methods

Study sites and sampling

A total of 12 sea-bed video observing transects were conducted at 9 stations using a ROV ("Sprint 101"). The sampling locations are shown in Fig. 1. With the exception of station ANT XIII, 24II where an unusually long video observation was split into four different transects, each single station comprised one video transect, in total lasting approximately 60 minutes. The length of the transects was determined by the drift of the ship and the width (ca. 0.5 m) was estimated by two parallel laser beams, which acted as a scale on the image. Comparable sample sizes were obtained by randomly selecting video footages from the complete transects being as continuous as possible and representing 150 m of seafloor for the analyses.

In the Weddell Sea, video records were taken during the expeditions ANT XIII/3, ANT XV/3 and ANT XVII/3 of the German R/V “Polarstern”. For details on the expeditions see Arntz and Gutt 1997, 1999; Arntz and Brey 2001. One study site is situated at stn 059-1 and west of Atka Bay stn 32IV. At the first station the seafloor rises continuously at a width of approximately 5 km towards the ice-shelf coast, where the ice is locally in contact with the approximately 55 m deep sea-floor (Grosfeld et al. 1989). The site off Kapp Norvegia is an unusually shallow bank

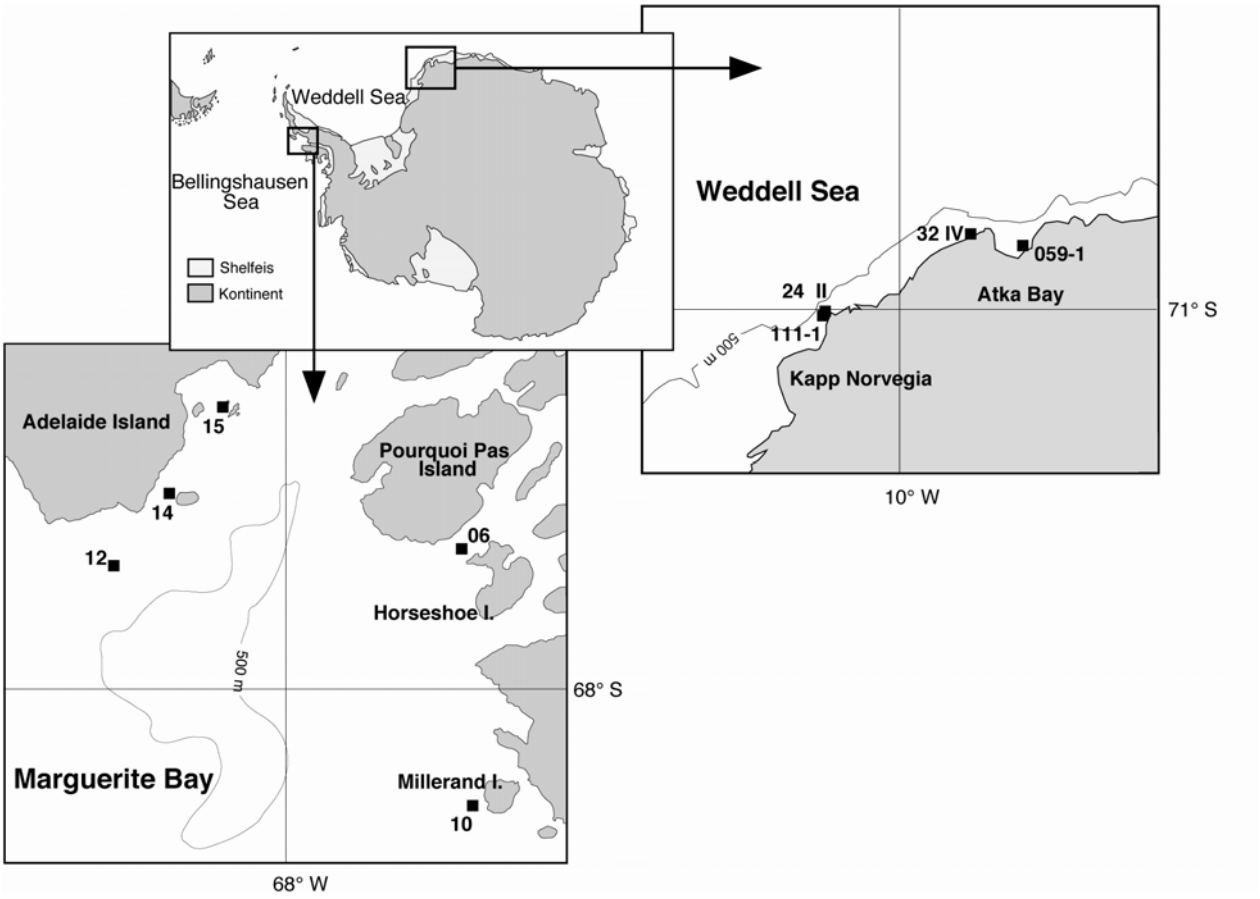


Fig. 1 Areas of investigation: Bellingshausen Sea (Marguerite Bay) and Weddell Sea (Atka Bay, Kapp Norvegia), Antarctica

with a marked topography off Four Seasons Inlet (11°28'W 71°07.5'S) NE of Kapp Norvegia (Fig. 2). This bank is approximately 1.7 km long in its north-west south-east extension and on average 320 m wide; it rises from a plateau at 170 m depth to 60 m depth at its shallowest part. Its north-eastern slope is relatively steep over the complete depth ranging from approximately 150 to almost 60 m. Here the long video observation (ANT XIII, stn 24II) was separated according to depth into three separate transects representing single samples. The southwestern slope is steep only in shallow water between 60 and 90 m where one additional transect had been videotaped (ANT XVII, Stn 111-1). Another transect at this side of the bank is from a more gentle slope at around 120 m depth (end of stn 24II).

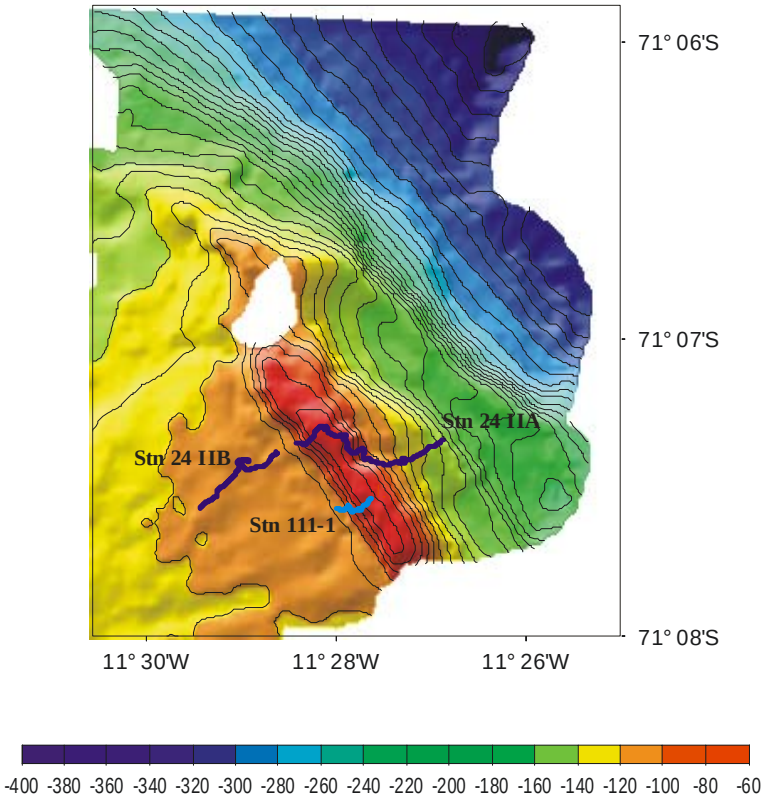


Fig. 2 Multibeam bathymetric map of Four Seasons Bank (Weddell Sea), showing video transects from ROV ("Sprint 101")

In the second study area, northern Marguerite Bay (by Adelaide Island) off the west coast of the Antarctic Peninsula (Fig. 1), video transects were undertaken from the British Antarctic Survey research vessel R.R.S. "James Clark Ross" (cruise JR37). The land as well as the seascape, and consequently the coastline, are here quite variable and heterogeneously structured. The transects covered depths below 57 m. The 160 m depth contour was defined as the lower depth limit for this study at all three sites.

Faunal analysis

All organisms > 1 cm were counted and identified to the lowest possible taxonomic level at the given optical resolution of the cameras. Colonies of colonial taxa were counted and treated as single individuals in the statistical analyses. Where this approach proved impossible because of the irregular shape of the colony, percentage cover of the sea floor was determined and used as a proxy for true abundances. In order to achieve a better identification of the organisms, an

average of 100 still photographs for each station also made by the ROV on the same transects were consulted in addition to the video observations.

Data analyses

For horizontal seriation and species turnover analyses, the 150 m long seabed video-strips were divided into 15 continuous areas, here defined as subsamples of 5 m^2. For depth zonation complete transects were chosen and divided into continuous subsamples of 15 m^2 each.

Classification and Ordination. Multivariate analyses were based on a matrix containing abundances for each subsample. Square root transformation was used, to reduce the contribution from numerically dominant species and to reveal changes among less dominant species (Field et al. 1982). Similarities between stations and taxa were calculated using the Bray-Curtis coefficient. A hierarchical agglomerative cluster analysis (i.e. classification) was used and the linkage option was the group-average method, which is more balanced and produces a moderate number of medium-sized clusters that are only grouped at a later stage. Non-metric multi-dimensional scaling (MDS; Kruskal and Wish 1978) was employed for ordination. This method plots complex multivariate relationships in two dimensions. A low MDS stress coefficient of <0.2 indicates that the multivariate similarity pattern is represented by the plot without much distortion (Clarke 1993). Cluster analysis and MDS were applied for both horizontal seriation and vertical zonation.

Horizontal seriation. For seriation analyses all 12 sea-bed video observing transects were used. The extent to which the communities change in a smooth and regular fashion (= degree of

seriation) was visualised by joining the subsamples in an MDS in their spatial order along the transects. An index of multivariate seriation (IMS) (Clarke et al. 1993) was calculated to determine the extent to which the species compositions depart along the transects from their state at the start of transects. The IMS is obtained from a Spearman rank correlation coefficient (ρ) computed between the corresponding elements of two triangular matrices of rank dissimilarities. The first is that of Bray-Curtis coefficients calculated for all pairs from the *n* mega-epibenthic community (n=15) transect subsamples and the second is from the inter-point distances of *n* points laid out, equally-spaced, along a line (= transect). If changes in species composition match this spatial sequence then the IMS is close to 1. Alternatively, the IMS will be close to 0 if species composition along the transect does not show any discernible pattern: being possibly similar at opposite ends but very different in between. The percent significance levels calculated for each IMS are based on a Monte Carlo permutation test for absence of seriation (Clarke and Green 1988).

Species turnover. Species turnover or beta-diversity is the extent of change in species composition of communities among samples and, consequently, not related to the size of the area investigated (Whittaker 1975). As a measure of species compositions in the subsamples the Bray- Curtis similarities between all pairwise permutations were used. The higher the overall similarities are, the lower is the species turnover value (Magurran 1988).

Depth zonation and diversity. The video observations at the shallow bank off Four Seasons Inlet in the Weddell Sea provided the opportunity to study depth zonation because of the depth range of 61 to 143 m at its NE slope (transect 24IIA) and of 60 to 112 m at its SW slope

(transects 24IIB, 111-1). All these transects were analysed together and the continuous subsamples of 15 m^2 each were used to calculate a similarity matrix as a basis for multivariate analyses, MDS and cluster analysis. In addition, the latter was used for an inverse analysis (Field et al. 1982) in order to cluster taxa that tend to co-occur in similar ratios across subsamples. The resulting community table provides a good tool to explain the outcome of the MDS and clustering. In addition, univariate measures of taxa diversity and evenness were computed: total number of taxa (S) and Hill's numbers of diversity (N1= exp (H')) with $H'=-\Sigma_i p_i \ln(p_i)$ and p_i= relative abundance per station of species i(Clarke and Warwick 1994).

The majority of the techniques are described in Clarke and Warwick (1994) and were implemented using PRIMERv5 (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley 2001).

Results

Horizontal seriation

Seriation values (ρ) and their significance levels, are shown in Table 1. No single transect covered a depth range broader than 137 m. In the Marguerite Bay (stns 006, 010, 012 and 014) seriation varied to a large extent, ranging from 4 significant values to the lowest non-significant result.

Table 1 Index of Multivariate Seriation (IMS) for each station. Values in parentheses are the % significance levels based on a permutation test for absence of seriation (M=999 simulations)

	Station	IMS
Marguerite Bay	006	0.19 (3.7%)*
	010	0.38 (0.7%)*
	012	0.42 (0.3%)*
	014	0.22 (2.8%)*
	015	0.16 (7.5%)
Atka Bay	059-1	0.15 (8.6%)
	32 IV	-0.02 (55.7%)
Four Seasons Bank	111-1	0.33 (0.3%)*
	24 IIA-S	0.46 (0.3%)*
	24 IIA-MS	0.50 (0.2%)*
	24 IIA-D	0.62 (0.1%)*
	24 IIB	0.07 (24.9%)

For three examples from this investigation area also the MDS plots are shown. At stn 012 (Fig. 3a) 15 subsamples along the transect conform rather closely to a linear sequence, and there are no strong discontinuities in the sequence of community change (i.e. no discrete clusters separated by large gaps); the community change follows a quite gradual pattern (Fig. 4a-b). At this station subsamples 9 and 14 could be regarded as “outliers” of the seriation showing lowest taxa numbers (S) and a very low abundance of sedentary Polychaeta sp.1 (Fig. 4c). However, these two subsamples did not exhibit any special relations with sediment, currents or ice scouring.

Stn 010 also showed horizontal seriation although the MDS plot did not depict a linear sequence (Fig. 3b). Great part of the sediment at subsamples 1-9 is conformed by sand valleys and sand crests, but beds of shells of *Adamussium colbecki* are also present (Fig. 5a-b). At subsamples 10 and 11 begins a mixture of sand with pebbles and cobbles to appear. Most of the substrates at

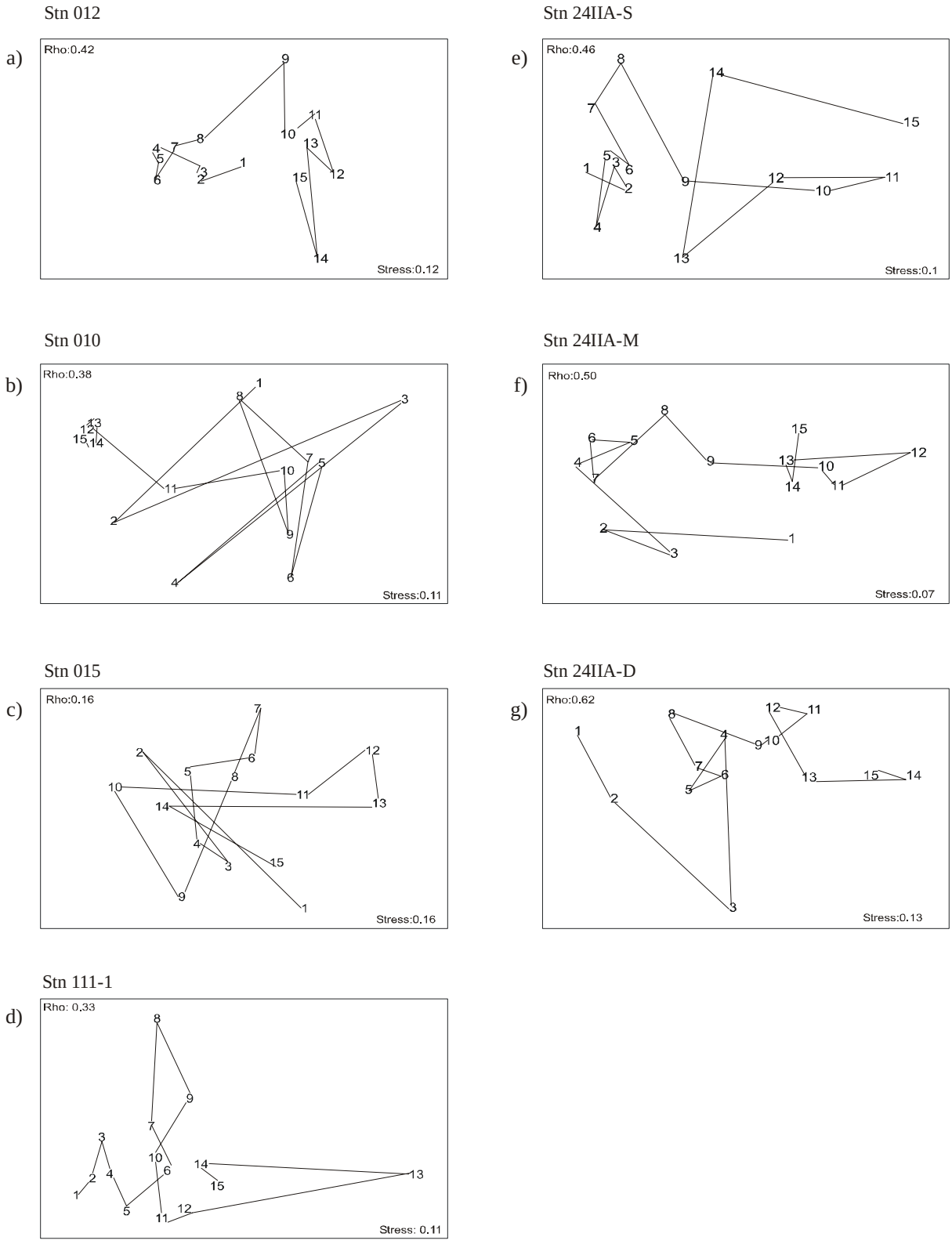
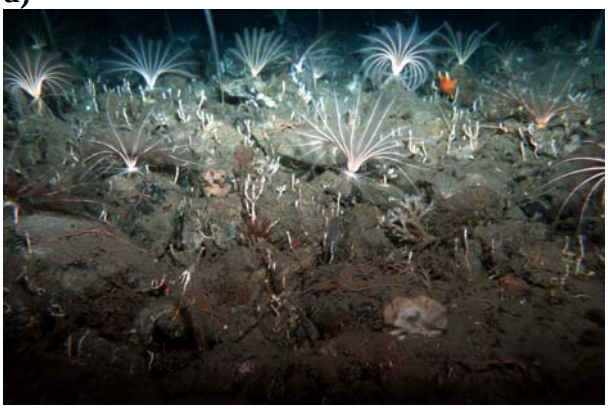


Fig. 3 Multi-dimensional scaling (MDS) of the mega-epibenthic communities in the Bellingshausen (**a-c**) and Weddell (**d-g**) seas, based on Bray-Curtis similarities from root-transformed data on abundances. The lines indicate the degree of seriation by linking successive subsamples along the video transect. The *Rho* values are Spearman correlation with a linear sequence (the IMS).

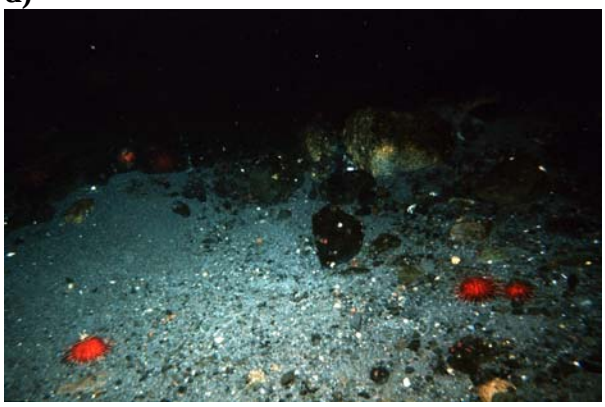
Stn 012

Stn 24II shallow

a)

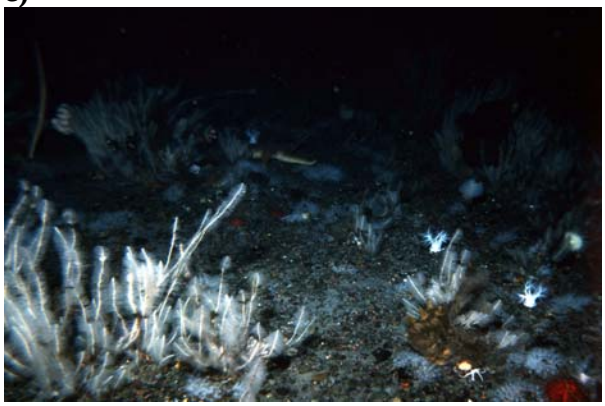


d)



b)

e)



c)

f)

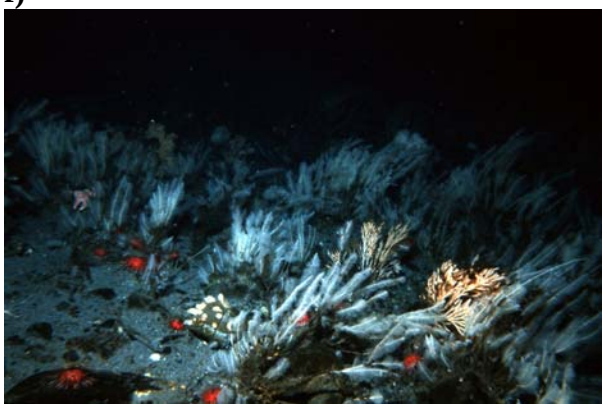
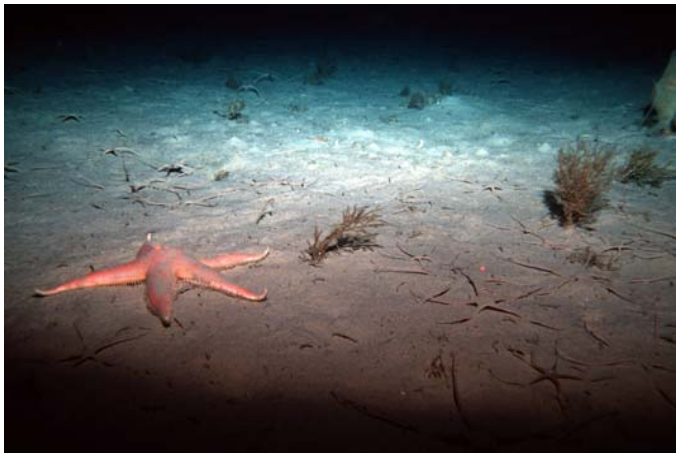
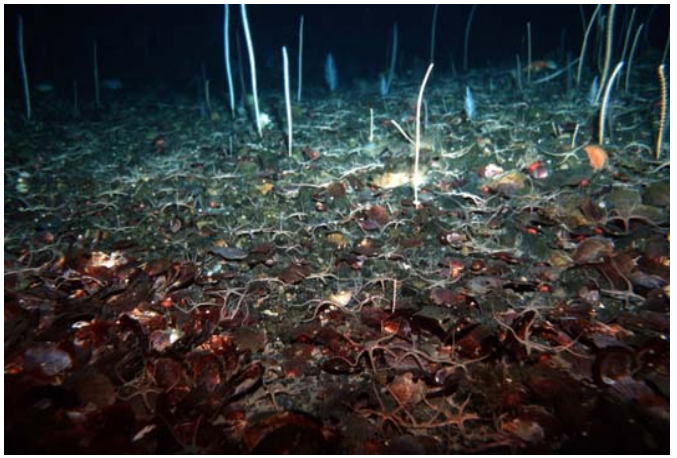


Fig. 4 Horizontal seriation in the Bellingshausen (stn 012) and Weddell Seas (stn 24II-shallow), photographic representation of some of the outliers in the seriation. **a)** and **b)** show part of the community structure present at the majority of the subsamples, with high abundances of the sedentary Polychaeta sp.1, (106 m). **c)** Represents outliers of the seriation (subsamples 9 and 14) showing low abundances of the Polychaeta sp.1, (102 m). **d)** Ice scour (58 m), with low abundances of *Oswaldella antarctica* (hydrozoa) (subsamples 7-8). **e)** and **f)** display differences in abundances of *O. antarctica* and sediments between different subsamples, (60 and 59 m).

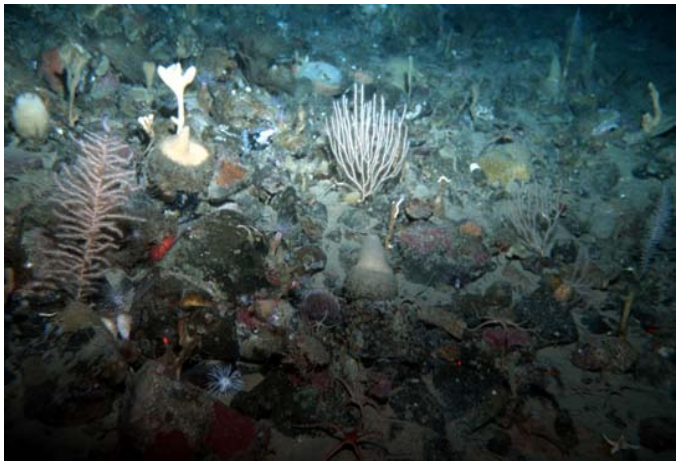
a)



b)



c)



d)

Fig. 5 Horizontal seriation in the Bellingshausen Sea (Marguerite Bay, stn 010): photographic representation of the substrata of the subsamples. **a)** Sand bottoms, with valleys and crests, (80 m). **b)** Shell-beds of *Adamussium colbecki*, (70 m). **c)** and **d)** mixture of sand with pebbles and cobbles, (77 and 73 m).

subsamples 12–15 are pebbles and cobbles with a very small amount of sand (Fig. 5c-d). This explains the proximity of the latter subsamples displayed in the MDS plot.

At stn 015 (Fig. 3c), no seriation was observed which becomes obvious from the irregular arrangement of the subsamples in the MDS-plot. The points representing the species compositions "jump" irregularly and show a very heterogeneous non-continuous pattern. The IMS had a low value (0.16) and the correlation with a linear sequence is no longer significant (ρ=7.5%).

Stations 059-1 and 32IV situated in the Atka Bay did not show any horizontal seriation pattern. The MDS plots look similar to that of stn 015 (Marguerite Bay) and are therefore not shown. At the Four Seasons Bank for all four stations/transects with relatively high and significant seriation values, ranging from 0.33 to 0.62 also the MDS plots are presented (Fig. 3d-g). Despite the overall trend within each transect of a good correlation between the faunistic composition and the linear sequence (seriation), local deviations from this general pattern become obvious, e.g. subsamples 8, 9 and 13 at stn 111-1, 12-15 at stn 24IIA-shallow, or 3 at stn 24IIA-deep.

Station 111-1 did not show any visible ice scouring or influence of strong currents and the sediment was very homogeneous along the whole transect. Differences of "normal subsamples" with the "outliers" (8, 9, 13) might be explained by differences in species abundances. Subsamples 8 and 9 showed low abundances of the hydroid *Schizotricha* sp.2 and the octocoral *Clavularia* cf. *frankliniana,* and no presence at all of the hydroid sp.8. Subsample 13 displayed low abundances of *Schizotricha* sp.2 and no presence at all of *C.* cf. *frankliniana* and the hydroid

Stn 24II middle

Stn 24II deep

a)

d)

b)

e)

c)

f)

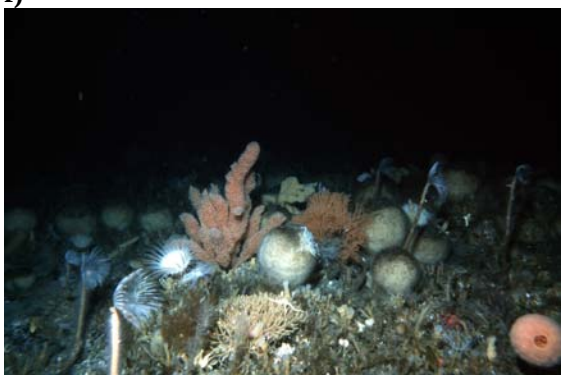


Fig. 6 Horizontal seriation in the Weddell Sea (Four Seasons Bank), photographic representation of some of the outliers in the seriation. *Mid-depths*: **a)** Assemblages of gorgonians (120 m) present where strong currents are absent (subsamples 1-3), conversely, assemblages of subsamples 4-12 (**b** and **c**) present at sites characterized by strong currents, (118 and 95 m). *Deep sites*: **d)** Displays subsample 3, with absence of *C. barbata* (Demospongiae, 129 m), which is present at subsamples 1-2 (**e** and **f**), (128 and 130 m).

sp.8. It also showed high abundances of the hydroid *Oswaldella antarctica* and the sedentary Polychaeta sp.1. The hexactinellid sponge *Rosella racovitzae* and the bryozoan *Bostrycopora dentata* were only present at this subsample.

At station 24IIA-shallow subsamples 7 and 8 are ice scours (Fig. 4d). Subsamples 12 and 15 are characterized by high abundances of *O. antarctica*. Conversely subsamples 13 and 14 showed low abundances of *O. antarctica*, the sediment is different compared with the other subsamples and is conformed by pebbles and boulders (Fig. 4e-f). At station 24IIA-middle subsamples 1-3 do not show strong currents (Fig. 6a), which are very characteristic of the subsamples 4–12 (Fig. 6b-c). Subsample 15 is an ice scour, which differentiates faunistically but not very clear by subsamples 13 and 14. Characteristic at station 24IIA-deep is that subsample 3 lacks the presence of the sponge *Cinachyra barbata* (Fig. 6d) the abundance of which is clear at subsamples 1 and 2 (Fig. 6e-f).

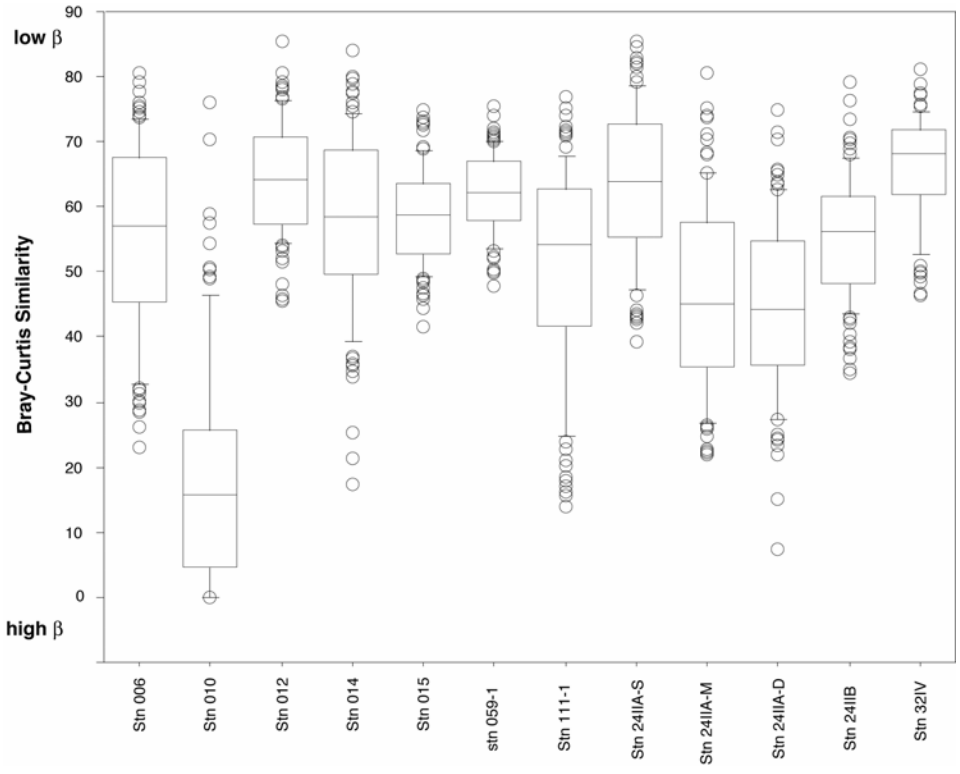


Fig. 7 Species turnover. Distribution of similarity coefficients between all possible combinations of subsamples. Box Plots: the 5 horizontal lines represent 10th, 25th, 50th, (median), 75th and 90th percentiles of the variable; circles represent outliers. Sample size (n)= 15 for each station. (*S* shallow; *M* middle; *D* deep; *B* transect on the south-west slope).

Fig. 7 shows species turnover within transects by use of Bray-

Curtis similarity medians. No general trend is discernible. The lowest median values, representing high species turnover are displayed by stations 010, 24IIA-middle and 24IIA-deep. Station 32IV shows the highest median, indicating a very low value for species turnover. Single consistencies of these results with those from the seriation analysis or corresponding discrepancies are pointed out in the discussion since they can provide insight in the ecological background of specific patterns.

Depth zonation

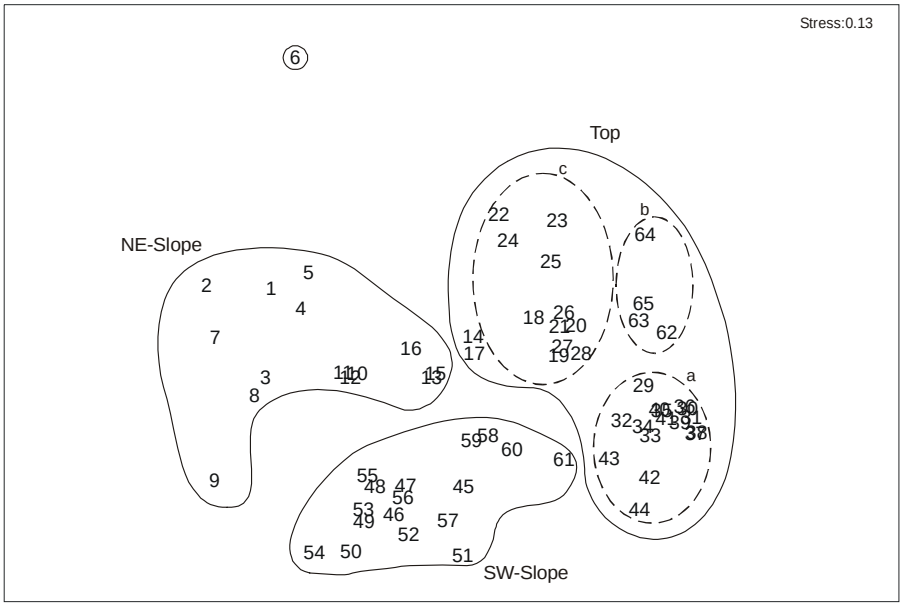


Fig. 8 Nonmetric Multidimensional Scaling (MDS) ordination based on Bray-Curtis similarity derived from root-transformed data at Four Seasons Bank in the Weddell Sea, Antarctica. Dotted lines represent subgroups formed at the "Top" of the bank: a, b and c

In the MDS ordination plot combining all subsamples at the Four Seasons Bank three main groups were separated: "Top", NE "Slope" and SW "Slope" (Fig. 8), using information from the cluster analysis.

These groups coincide very well with the location on the bank and are therefore labelled accordingly. Quite obvious is the difference between the SW and NE slopes with a higher heterogeneity at the NE slope. The information on the SW slope is from two different transects of which the total of the subsamples form one group. In both groups a depth gradient is visible with the shallow subsamples on the right and the deeper on the left side of the MDS plot. The "Top" group shows the largest heterogeneity; the links with both slope gradients along the transects are not very obvious, in case of transect 24IIA consisting of "Top_a" (59-77 m), "Top_c " (82-105 m) and the "NE slope" (111-146 m) or even interrupted in case of the transect of stn 111-1 comprising "Top_b" (53-57 m) and the shallower subsamples of "SW slope" (56-89 m).

Figure 9 shows a condensed community table of the fauna observed at Four Seasons Bank, based on cluster analyses for subsamples and species. At the “Top” we found a typical shallow-water fauna characterized by species as the octocoral *Clavularia* cf. *frankliniana*, and locally high abundances of the hydroid *Tubularia ralphii* as well as the sea urchin *Sterechinus neumayeri* (Fig. 10a-c). The local variations within the taxa group B1 especially of the two latter species and in addition the almost unique high abundance of *Ainigmaptilon antarcticum*, *Corymorpha parvula*, Hydrozoa sp.8 and *Corymorpha* sp.1 in subgroup b explain the separation of the subgroups a-c within “Top”.

The NE “Slope” displayed a small proportion of the shallow-water fauna but is dominated obviously by a typical slope mega-epifauna (B2) of which the taxa Gorgonaria sp.11, Sabellidae spp., Crinoidea spp., *Tedania tantula*, *Primnoisis* spp., *Thouarella* spp., *Dasystenella* spp. have highest abundances only at this slope, and is also characterized by scattered presences of taxa

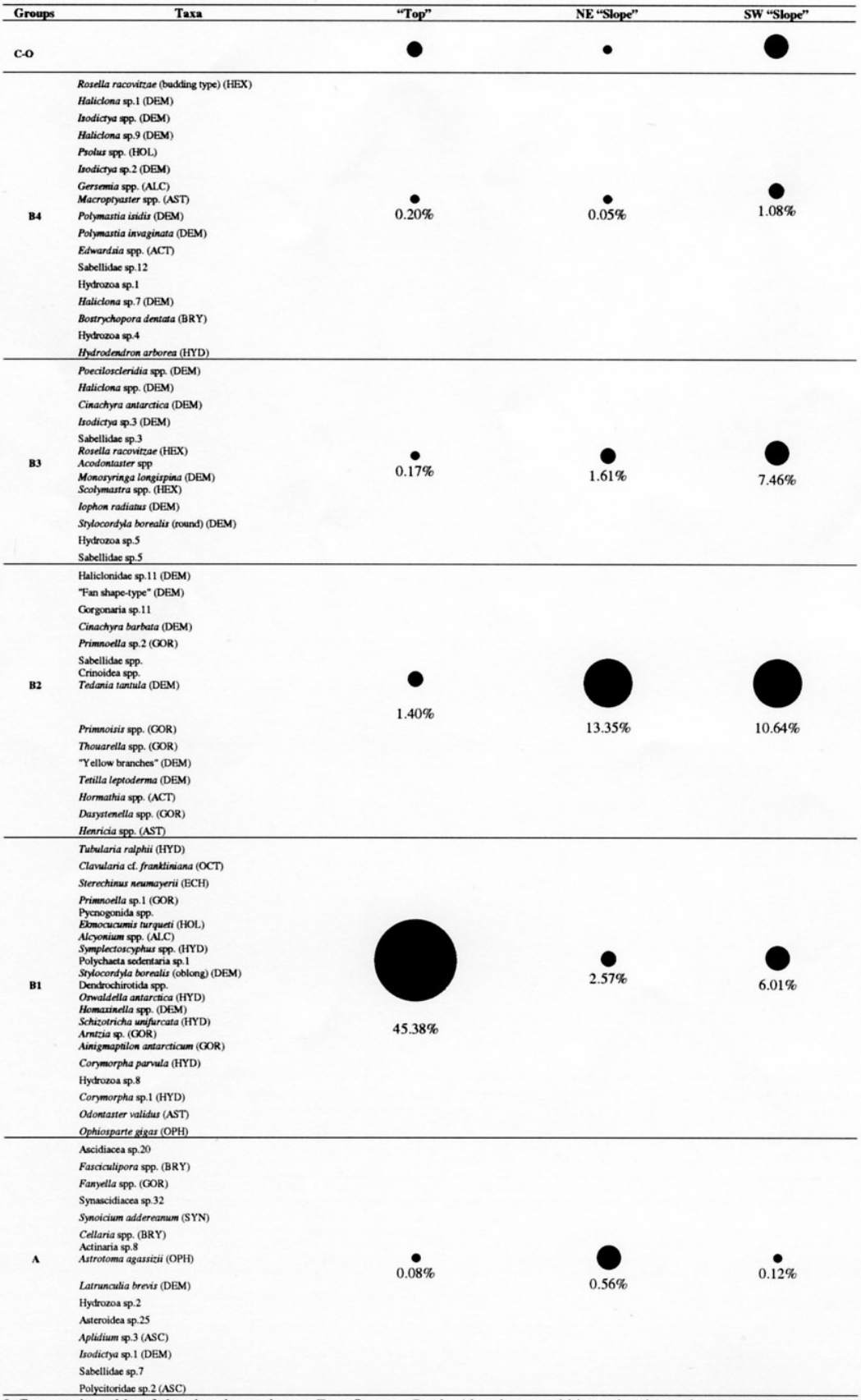
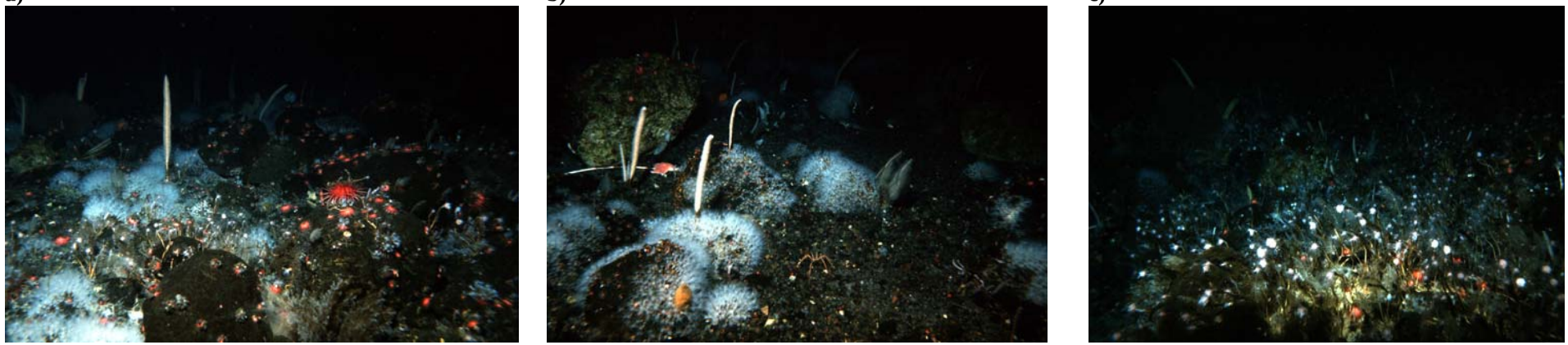


Fig. 9 Community table of the abundance data at Four Seasons Bank. Abundances within each subsample group per taxa group are depicted by the size of full circles. Taxa and subsamples ordered according to cluster analysis, R-mode and Q-mode, respectively. Taxa were classified into three groups at 35% similarity. At 18% similarity 18 groups can be distinguished of which C to O consist of only a maximum of 39 taxa with generally low presence and abundances; Presences results for these groups are condensed to one line.

Top

a) **b)** **c)**



Northeast-slope

d) **e)** **f)**

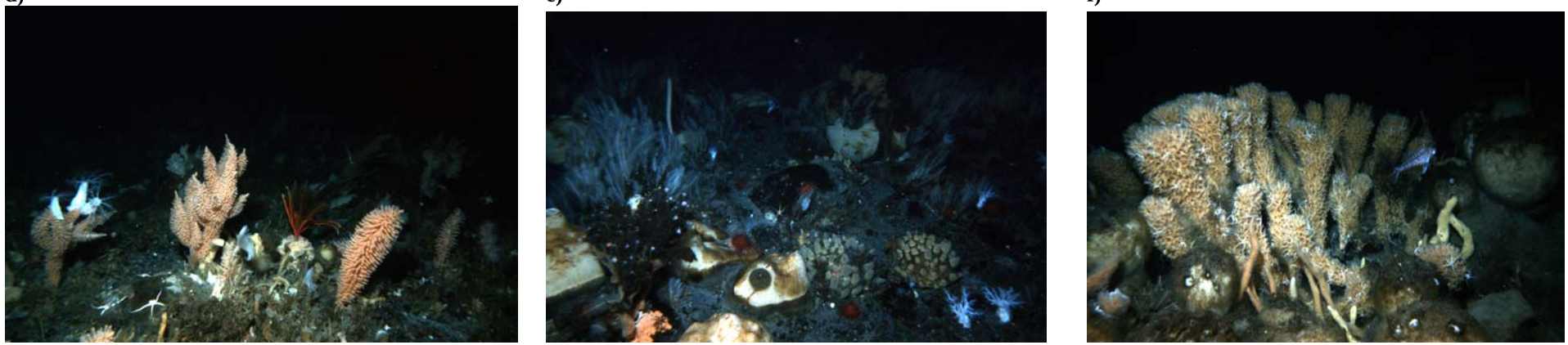


Fig. 10 Photographic representation of groups obtained by MDS ordination at Four Seasons Bank. *Top* **a)** and **b)** Boulders and gravel sediments with *Clavularia* cf. *frankliniana* (Octocorallia), *Sterechinus neumayeri* (Echinoidea) and gorgonians, (62 m) **c)** *Tubularia ralphii* (Hydrozoa), (63 m). *Northeast-slope* **d)** *Thouarella* spp. (Gorgonacea), Crinoidea spp., (129 m) **e)** *Polymastia invaginata*, *P. isidis* (Demospongiae) and *O. antarctica* (Hydrozoa), (60 m). **f)** *Isodictya* spp. and *C. barbata* (Demospongiae), (109 m).

Southwest-slope

a) **b)** **c)**

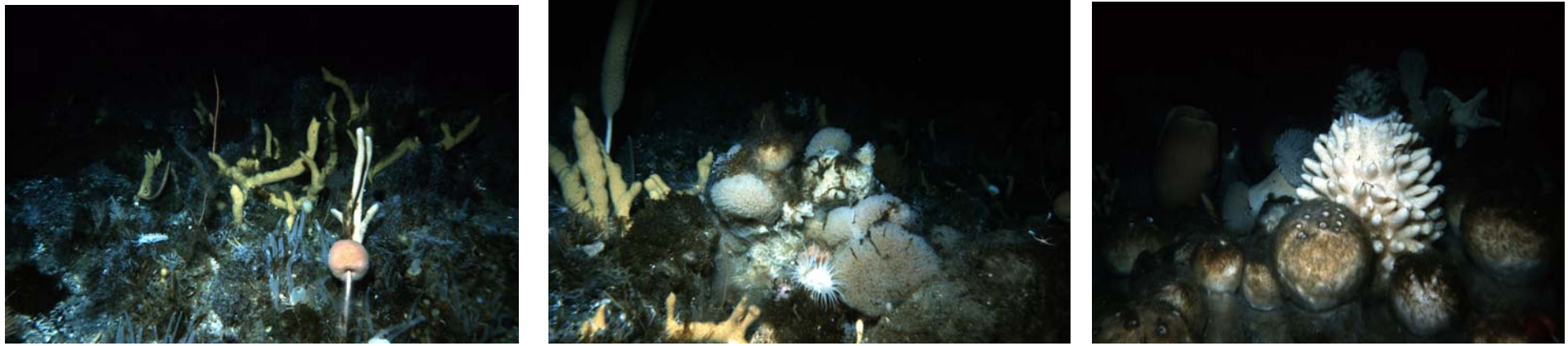


Fig. 11 Photographic representation of groups obtained by MDS ordination at Four Seasons Bank. *Southwest-slope* **a)** *Monosyringa longispina*, *Stylocordyla borealis* round, "Yellow branches", (110 m). **b)** Demosponge assemblages, (108 m). **c)** *C. barbata* (Demospongiae) and hexactinellid sponges : *Rosella racovitzae*, *Scolymastra joubini*, (109 m).

belonging to the taxa group A with e.g. *Fanyella* spp., Synascidiacea sp.32, Actinaria sp.8, *Latrunculia brevis*, *Aplidium* sp.3, *Isodictya* sp.1 (Fig. 10d-f). The SW "Slope" showed a most homogenous fauna without a specific dominance of species groups being especially characteristic of any single depth stratum or local area (Fig.11).

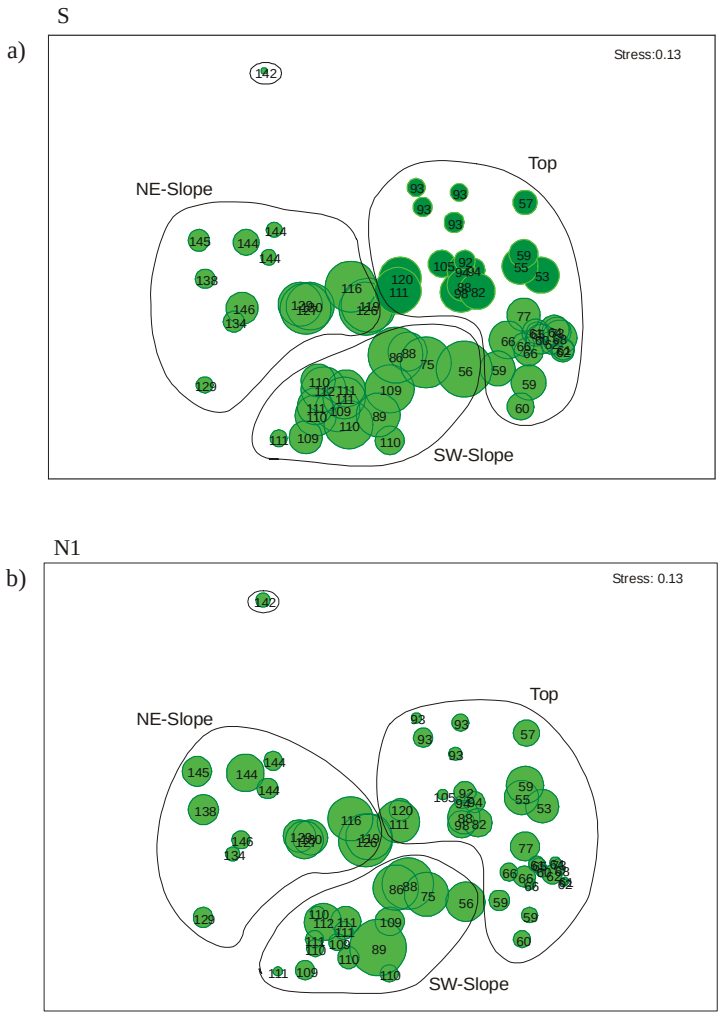


Fig. 12 MDS ordination based on Bray-Curtis similarity derived from root transformed abundance data at Four Seasons Bank in the Weddell Sea, Antarctica. Subsamples have been with depth labels superimposed. Circles sizes represent values for number of taxa (S) and diversity (N1)

Numbers of taxa and univariate measures of diversity of the Four Seasons Bank are displayed in Figure 12. Numbers of taxa and diversity are superimposed on the subsamples (each 15 m^2). Values of number of taxa varied between 4 and 35. For the diversity 16.2 was the highest value and 2.1 the lowest. Considering the three main groups: "Top", NE "Slope" and SW "Slope", the highest number of taxa was observed at the SW "Slope" and also the highest values for diversity. Moderate and small values of number of taxa were displayed at the "Top" but diversity values were very low. On the

contrary the NE “Slope” showed the lowest values but also high values of number of taxa, and diversity values were higher than at the “Top”.

Also two characteristics of the diversity are remarkable in Figure 12b. At the northern site of the bank diversity increased with increasing depth. However, at the southern site of the bank no trend is discernible and the highest diversity values can be observed at mid-depths.

Discussion

Horizontal Seriation

Specific seriation patterns of benthic ecosystems may be caused by both abiotic conditions (depth, substratum, habitat, bottom topography, sedimentation, oceanography, disturbance) (Dayton et al. 1970, 1994, Gallardo 1987, Barnes et al. 1996, Gutt 2000) and by biotic factors (competition, predation, recruitment) (Rowe 1981, Arntz et al. 1994, Clarke 1996a, 1996c).

Benthic processes seem to be very complex in the Antarctic and, consequently, it was not the aim of this study to reveal general correlations between benthic structures and biological as well as chemico-physical processes. Nevertheless, explanations for both, significant and non-significant seriation can be provided. Stations with the poorest seriation, e.g. stn 015, 059-1, and 32IV belong to those with the smallest range of species or faunal-heterogeneity but with intermediate values for species turnover (median of Bray-Curtis values). This shows that along the 150 m standardized transects neither a patchwork of different assemblages nor a gradual

change in assemblages exists, instead the fauna is quite homogenous. This phenomenon was observed locally in all three areas of investigation. Interestingly, this includes two stations (059-1 and 32IV) which are situated close (<0.5 km) to the ice shelf coast, where, due to a continually changing environment, greater differences in benthic communities can be expected than elsewhere or at different spatial scales (Barry and Dayton 1988, Gutt 2000).

Discontinuity in the mega-epibenthic assemblages may correspond to a sharp change in local bottom topography (Pérès 1982). Some of the stations analysed in Marguerite Bay displayed abrupt changes in the bottom topography, e.g. stn. 010. Soft-bottom sediments with valleys and crests, drop stones, and biogenic substrata (e.g. scallop shells of *Adamussium colbecki*) were observed along this transect.

An exceptional result in terms of species turnover is that of stn 010, with a high heterogeneity, whilst the IMS value and its significance level were intermediate. Here obviously changing environmental conditions at different levels shape a heterogeneous megabenthos. The fauna seems to exhibit both a gradual change in taxa composition and, superimposed, a faunal patchwork shaped by discrete impact independently of the locality on the transect.

Four transects, one from the Marguerite Bay and three from the Four Seasons Bank, show relatively good faunal seriation, though, never high values close to 1.0. The latter transects have broad ranges of species turnover values. Because of the mathematical nature of the IMS this combination of median and value range can be found if an existing seriation is occasionally interrupted. At both sides of the Four Seasons Bank the most obvious disturbance agent is

iceberg scouring, a process which also leads to the heterogeneity within the two groups of subsamples, SW-slope and NE-slope, the latter including one subsample with an extreme faunistic composition. The same was observed in the "Top" group where additional disturbance, such as wave action, an especially strong exposure to tidal and other currents, changes in daylight and a more intensive ice impact due to shallow water depth is obvious. The fact that nevertheless a significant seriation existed might be due to the small but not avoidable depth gradient within each depth stratum (=transect, 24IIA-shallow, 24IIA-middle, and 24IIA-deep), causing gradients in ecologically relevant conditions as also observed at a larger spatial scale discussed below. In contrast to all the other results discussed above stn 012 in Marguerite Bay has a relatively high median value of species turnover, with a narrow range of corresponding single values. This can be explained by an obviously very good seriation, however, without a very clear faunal difference between the beginning and the end of the transect and not being considerably interrupted. Furthermore there was no indication of any change in the abiotic environmental conditions. This is confirmed by the horseshoe-shaped MDS plot, a pattern which is typical of temporal succession rather than for the spatial structure found here.

Depth zonation

Clear zonation according to depth has been observed by different authors (Rowe and Menzies 1969, Dayton et al. 1970, 1974, Carey et al. 1975, Piepenburg and Schmid 1996, Mayer and Piepenburg 1996). Vertical distributions of benthic communities (0-150 m) in Terra Nova Bay (Ross Sea) (Cattaneo-Vietti et al. 2000a) displayed some similarities with the pattern observed at Four Seasons Bank. At depths between 2 and 70 m the sea urchin *Sterechinus neumayeri* is also

abundant; below this depth range (up to 150 m) a complex community of sponges and anthozoans characterize the area. The sponge community living at Four Seasons Bank is quite similar to those found at McMurdo Sound: mixed and glass sponge communities (Bullivant 1967, Dayton et al.1974), but at both sides of the bank (NE and SW "slopes") high abundances of single species like *Cinachyra barbata*, *Stylocordyla borealis* (round type), *Tedania tantula*, *Monosyringa longispina*, *Polymastia invaginata*, *Polymastia isidis* are remarkable.

In general, the Four Seasons Bank seems to comprise several faunal assemblages which combines a clear depth gradient and a zonation with discrete assemblages. Special environmental conditions are originated due to the topography of the bank. Strong currents and a generally enhanced variability on banks have been observed frequently (Genin et al 1986; Beckmann 1999). Hydroids (*Tubularia ralphii*, *Oswaldella antarctica*, *Corymorpha parvula*, Hydrozoa sp.8 and *Corymorpha* sp.1) and anthozoans (*Clavularia cf. frankliniana*), especially gorgonians (*Ainigmaptilon antarcticum*, *Primnoisis* spp., *Thouarella* spp., *Dasystenella* sp., *Fanyella* spp.), were well represented. Some of these species are described as "macro"- and microphagous" suspension feeders whose feeding strategies imply that sediment might be resuspended e.g. by the effect of currents (Orejas et al. 2001, 2003) and that other methods than active filtration (e.g. gravitational deposition, direct interception) may also occur (LaBarbera 1984). In this context, strong currents seem to be an advantage for the establishment of this group of organisms because these currents supply them with food (Genin et al 1986, Rogers 1994).

Depth zonation and diversity values observed appear to be affected by the nature of the substratum (cf. Pérès 1982, Kirkwood and Burton 1988, Hecker 1990, Simboura et al. 1995,

Nonato et al. 2000). The lowest values were displayed in shallow areas at the northern site of the bank where boulders and pebbles were the main substrata. This type of substrata favoured epilithic organisms or species that need a form of anchorage for their settlement; e.g. the octocoral *Clavularia* cf. *frankliniana* forms encrusting colonies that cover a great part of the stone (Gili et al. 1999) and the hydroid *Tubularia ralphii* forms creeping colonies on stones (Stepaniants 1980).

The complex morphology and architecture of specific organisms (e.g. sponges, gorgonians, bryozoans, ascidians) offer a variety of secondary habitats providing favourable conditions for epibiotic species (Gutt and Schickan 1998). This might explain high values of diversity and number of taxa observed at both sides of the bank (NE and SW "slopes"), where sponges were abundant. Sponges provide the most fascinating of these secondary habitats in Antarctica (Arntz et al 1997, Gutt and Schickan 1998), being associated with a large number of organisms that exhibit epibiotic behaviour (Gutt and Schickan 1998). These associations generate a variety of "multi-storied habitats" and living substrates provide additional ecological niches (Gutt 1996).

Furthermore current regimes are also responsible for faunistic differences found between the northeast and southwest "slopes". The bank is situated in an area that is affected by the Antarctic Coastal Current and water coming out the Quarisen ice shelf (Fahrbach et al. 1992, Dijkstra 2000). Therefore the east side of the bank is exposed to strong currents flowing through and flowing out the Quarisen ice-shelf. As the strong Antarctic Coastal Current reaches the northward tip of the bank, it starts to flow southwest decreasing velocity. As a consequence, the western side of the bank is sheltered from these strong currents and may also be protected, by the

east side, from the high frequencies of iceberg impact. This might explain the higher heterogeneity found at the northeast “slope”.

In general these findings show, that despite the isolated nature of the Antarctic ecosystem, each detailed look at mega-epibenthic assemblages provides more insight into a high complexity of processes behind spatial structures. Our results do not only provide evidence that the high Antarctic benthos is not homogenous as indifferently stated some decades ago. They also show that the opposite, “all patterns can occur everywhere” as stated in some more advanced studies (Gutt and Piepenburg 2003), is not a general phenomenon if results refer to comparable spatial scales. Instead, different kinds of patterns are identifiable: a locally limited typical fauna, a patchwork of assemblages as well as continuous faunistic gradients. Combinations of these three scenarios are possible or must even be considered as the rule.

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Publication III

Differences in mega-epibenthic diversity on polar shelves at different spatial scales

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Abstract

Diversity of mega-epibenthic assemblages in the Arctic (off northeast Greenland) and Antarctic (Bellingshausen and Weddell Seas) was studied using underwater video. A total of 54 sea-bed video transects were conducted at 51 stations at depths between 35 and 585 m. At a regional scale (γ-diversity) Antarctic studied sites were richer in the number of mega-epibenthic taxa than the Arctic. In the Antarctic all regional species numbers in the shallow sites were higher than at deeper ones, but in contrast to the Arctic this could not be explained by a higher species turnover. No differences were found in species turnover (β-diversity) between the Arctic and Antarctic. At the local spatial scale (α-diversity) species numbers were higher in the Antarctic compared to the Arctic, what might be a reflection of a clearly higher regional diversity. In addition, differences in the type of natural disturbances such as predation pressure or iceberg scouring are another reason for the higher local species numbers in the Antarctic.

Key words: Mega-epibenthos, Arctic, Antarctic, marine biodiversity, alpha diversity, beta diversity, gamma diversity, underwater video, ROV

Introduction

The more detailed information on biodiversity becomes available and analytical approaches are developed the more the relevance of details becomes obvious also when generalizations are requested. This includes the often mentioned difference between the Arctic and the Antarctic benthos (George 1977, Knox and Lowry 1977, Dayton 1990) as well as statements referring to a homogenous Antarctic benthos. At an evolutionary scale long-term stability but also specific dynamic processes such as the change between glacials and interglacials (Pianka 1978, Clarke and Crame 1989) contribute to the complexity not only of polar biodiversity patterns. Nevertheless, origins and evolution of the Arctic and Antarctic benthos are different (Dayton 1990). At the ecological level, disturbances (Gutt 2001) and consecutive faunal succession as well as local and regional environmental conditions shape benthic structures.

With this background Gray (2001) concluded that two basic considerations have to be taken in account when comparing the Arctic with the Antarctic: age and area. The benthic fauna of an area such as the Southern Ocean cannot be viewed in isolation, and it is pertinent to ask how the present Antarctic fauna is related to faunas elsewhere (Clarke 1996b). Following this argument a reasonable approach is to study the faunistic and environmental parallelism with the Arctic. The Arctic and Antarctic benthic faunas have been compared previously by George (1977), Knox and Lowry (1977), White (1984), Dayton (1990) and Piepenburg et al. (1997), and all have indicated high species richness and diversity in the Southern Ocean. Recent studies on Antarctic benthic diversity (Clarke and Johnston 2003, Gutt et al., *in press*) have been made in order to get a better approach to the existent taxa and their number of species.

A study based on a best possible methodological compatibility and modern analytical approaches was that of Starmans and Gutt (2002) in which not only well known assumptions, e.g. that of a higher benthic diversity in the Antarctic compared to the Arctic were confirmed and diversity measure was not only reduced to the counting of species numbers. Some interesting questions raised in this investigation could not be sufficiently answered due to the lack of results from shallow waters in both Antarctic study sites. In the meantime such data have been sampled in the course of a joint German-English initiative. Again sea-bed video recording was used for data acquisition firstly in order to provide comparable information. Secondly, diversity of species identifiable on videos was used as a proxy for the desired but never attainable complete and absolute diversity of thousands of mega-epibenthic species, since this selection is not biased by the "taste" of the investigator. The three main questions (1) - (3) with detailed hypotheses were: (1) Is the mega-epibenthos inhabiting the Antarctic shelf really more diverse than that of the Arctic, comparing only same depth strata? (a) At the local spatial scale there is no reason to assume generally a higher diversity in the Antarctic than in the Arctic. (b) Due to a more heterogeneous bottom topography in the Arctic comprising an off shore bank, trenches, troughs, a shelf ice barrier and shelf areas situated close to the coast but being exposed to the open ocean, which may have consequences for the current regime (Dayton et al. 1994, Piepenburg et al 1997), species turnover is expected to be higher in the Arctic than in the Antarctic, at least on the relatively flat Weddell Sea shelf. (c) Due to the long period of isolated evolution, however, at a large regional scale the Antarctic shelf benthos at any depth must be richer than the Arctic (Clarke and Crame 1997). (2) Does within each of the 3 study sites the shallow-water mega-epibenthos perform a higher heterogeneity than the benthos on the deeper shelves? (a) At a local spatial scale (α-diversity) the shallower benthos is poorer than the deeper. Reasons for this difference to be discovered in future process-oriented studies could be locally varying

combinations of ecological conditions, e.g. wave action, small scale current regime due to an uneven bottom structure, or phytoplankton production to which only a few locally varying species are perfectly adapted. (b) Due to the resulting hypothesized faunistic heterogeneity species turnover (β-diversity) should be higher at shallower sites. (c) As a consequence of these two assumptions, regional diversity could be roughly equal at both depth strata. (3) Following principally Hill's (1973) diversity concept of a gradient ranging from pure species numbers, followed by a function of both, species numbers and evenness to pure evenness, gradients of decreasing or increasing sensitivity of the above mentioned environmental conditions can be found.

Material and Methods

Study sites

Antarctic

The Antarctic sites selected for this study comprised the narrow shelf (<500 m) of the eastern Weddell Sea in the Atlantic sector of the Southern Ocean, and the shelf of the Bellingshausen Sea in the Pacific sector (Fig. 1).

Voß (1988) characterized the sediments of the eastern Weddell Sea by the presence of sandy bottoms, bryozoan debris, sponge spicule mats and a few stones. He described also for the first time the benthic assemblages and distinguished the “Eastern” and “Southern” assemblages as the major ones on the shelf of the eastern Weddell Sea, which were corroborated later by Galéron et

al. (1992), Piepenburg et al. (1997), Gutt and Starmans (1998) and Starmans et al. (1999) and reviewed by Gutt (2000).

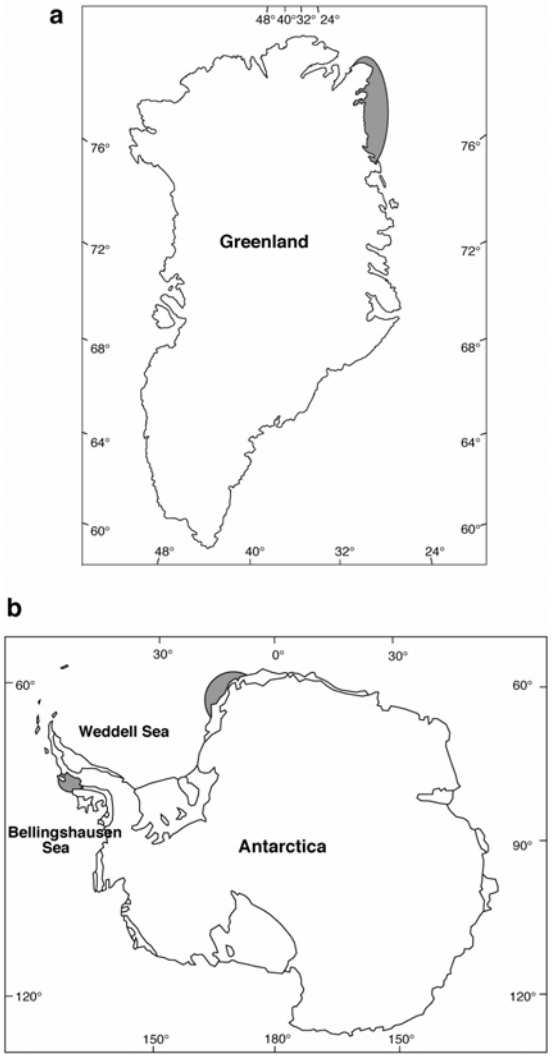

Fig. 1 Areas of investigation: a) off Northeast Greenland, b) Antarctica

Due to the submerged continental shelf and the glaciated coast shallow-water areas (<150 m) in the Antarctic are scarce. In the eastern Weddell Sea one two such sites are known, one in and west of Atka Bay and the other being a shallow bank off Four Seasons Inlet (11°28'W 71°07.5'S) NE of Kapp Norvegia, approximately 1.7 km long and on average 320 m wide, rising from a plateau at 170 m depth to about 60 m depth at its shallowest part.

In contrast to the Weddell Sea, the mega-epibenthos in the Bellingshausen Sea has been until now not intensively studied. Starmans et al. (1999) described the presence of sandy bottoms and the relative abundance of drop-stones. They remarked that the assemblages lacked the pronounced three-dimensional structure reported for communities in the Weddell Sea. Shallow-water stations (<150 m) in the Bellingshausen Sea were located in northern Marguerite Bay, where a true coast and adjacent shallow waters is normal in contrast to the eastern Weddell

Sea (Kennedy and Anderson 1989, Bonn et al. 1996). The land as well as the seascape, and consequently the coastline, are here quite variable and heterogeneously structured.

Arctic

The Arctic investigation site was the high-Arctic shelf region off northeast Greenland in the Greenland Sea (Fig. 1). At this site the bathymetry is complex and the shelf consists of a system of shallow banks (< 100 m) separated by troughs and trenches with depths >400m. Fine-grained sediments cover the sea floor, particularly in the shelf troughs and at the slope, whereas coarser fractions predominate on the shallower banks (Piepenburg 1988). Here a pronounced depth zonation is a principal feature of the megabenthic distribution (Piepenburg and Schmid 1996).

Field sampling

A total of 54 sea bed video transects were conducted at 51 stations using a ROV ("Sprint 101"). Stations were classified according to depth into shallower, 35-150 m, and deeper sites, 160-585 m, in order to get equally sized samples. Sea bed video records for both sites were carried out aboard the German R/V “Polarstern”. Deeper stations in the Antarctic were video-taped during the expeditions ANT VI/3 (eastern Weddell Sea) and ANT XI/3 (Bellingshausen Sea) (Fütterer 1988, Miller and Grobe 1996). Shallow–water samples in the eastern Weddell Sea were from the expeditions ANT XIII/3, ANT XV/3 and ANT XVII/3 (Arntz and Gutt 1997, 1999; Arntz and Brey 2001). Arctic samples for both depth ranges were taken off (Northeast Greenland, Greenland Sea) during ARK IX/2-3 (Hirche and Kattner 1994). Video transects in shallow water in the Bellingshausen Sea (Antarctica) were a major contribution to a bilateral project

between the Alfred Wegener Institute for Polar and Marine Research and the British Antarctic Survey, the field work of which was carried out during the "James Clark Ross" cruise (JR37).

With the exception of the shallow station ANT XIII, 24II in the Weddell Sea where an unusually long complete video observation was split into four different transects, each station is comprised of a video transect lasting between 60 and 90 minutes. The length of the transects was determined by the drift of the ship and the width (ca. 0.5 m) by two parallel laser beams, which acted as a scale on the image. Comparable sample sizes were obtained by randomly selecting video footages being as continuous as possible and representing 100 m^2 of sea floor for the analyses.

The split of the three study sites (Weddell, Bellingshausen and Greenland Seas) into two depth strata each resulted in 6 sampling sites: Antarctic: Weddell Sea, shallow (60 to 150 m) and deep (195 to 555 m); Bellingshausen Sea, 55 – 150 m (shallow) and 160 - 585 m (deep); Arctic: Greenland Sea, shallow (35 to 125 m) and deep (180 to 334 m). Nine stations were randomly chosen for each of the 6 sampling sites.

Antarctic shallow-water samples from Weddell and Bellingshausen Seas are new. In order to provide an optimum in compatibility e.g. in terms of sample size, raw data from Weddell Sea (deep), Bellingshausen Sea (deep) and Greenland Sea (deep and shallow) (Starmans and Gutt 2002) were recalculated for the analyses.

Faunal analysis

All individuals > 1 cm were counted and identified to the lowest possible taxonomic level at the given optical resolution of the cameras. Colonies of colonial taxa were counted and treated as single organisms in the statistical analyses. Where this approach proved impossible because of the irregular shape of the colony, percentage cover of the sea floor was determined and used as a proxy for true abundances. In order to achieve a better identification of the organisms, an average of 100 still photographs for each station also made by the ROV on the same transects were consulted in addition to the video observations.

Data analyses

Different measures of biodiversity were performed at two spatial scales: local (within-habitat or α-diversity) and regional (within the whole study site or γ diversity) (Whittaker 1960). In contrast, between-habitat or β-diversity is the extent of change in species composition of communities among samples and, consequently, not related to the size of the area investigated (Whittaker 1975). Data were analysed according to univariate and multivariate measures in the following way:

Within-habitat (α) diversity

Firstly univariate measures of diversity and evenness were computed for each group of stations: total number of taxa (S), Shannon diversity ($H' = -\Sigma_i p_i (\log_e p_i)$) and Pielou's evenness ($J' = H' / \log_e S$) (Clarke and Warwick 1994).

Secondly the normalised expected number of taxa, calculated after Hurlbert's (1971) modification of Sanders (1968) rarefaction method was used. The rarefaction technique despite the justify criticism of Gray (1997), allows one to adjust a series of samples to a common sample size so that species richness can be compared among samples, with varying abundances (Krebs 1999). This method calculates the expected number of taxa, $E(S_n)$, in a reduced standardised sample of n individuals selected from the given sample. For the rarefaction approach a reduced number of individuals (n=70) was chosen which took into account the lowest abundances at each station.

Between-habitat (β) diversity

For species turnover or β diversity, a similarity matrix was constructed using fourth-root transformation in order to reduce the contribution from numerically dominant species and to reveal changes among less dominant species (Field et al. 1982). Similarities between stations and taxa were calculated using the Bray-Curtis coefficient. As a measure of β diversity the Bray-Curtis similarity between all pairwise permutations of sites was used. The higher the overall similarities are, the lower the β diversity (Magurran 1988).

For α and β diversity, non-parametric Kruskal-Wallis tests and post-hoc multiple comparison (after Nemenyi) were used to test the significance of differences ($p<0.05$) (Sachs 2002) between the 3 study sites and Arctic and Antarctic at same depth strata.

Regional (γ) diversity

In order to assess the γ diversity, different indices of diversity were computed. Assuming mainly independent data comparability between primarily single values (H', $E(S_{70})$ and J') for each investigation site jack-knifing was applied, since it provides standard errors. Series of jack-knife estimates and, based on these, pseudovalues were produced. The mean of these pseudovalues forms the best estimate of the statistic (Magurran 1988). All values are given as means (±standard deviation). Statistical significance was tested using analysis of variance (ANOVA) and post-hoc procedures (Tukey test).

As a second measure of γ diversity, non-parametric estimators of true species richness were computed (Colwell 1997). Parameters that are components of the abundance-based estimators (Colwell and Coddington 1994) are "singletons" (species represented by a single individual) and "doubletons" (species represented by only 2 individuals). Incidence-based estimators, considered "uniques" (species restricted to a single site) and "duplicates" (species occurring at exactly 2 sites only) (Colwell and Coddington 1994). The following statistical estimators (Colwell 1997) were computed, a) Abundance-based estimators: Chao1 and Abundance-based Coverage Estimator (ACE); b) Incidence-based estimators: Chao2, Jack-Knife1 (1^{st} order), Jack-Knife2 (2^{nd} order) and Incidence-based Coverage Estimator (ICE). Values obtained were means. For all calculations involving random orderings of the samples, 50 randomisations (without replacement) were used. Values of these true species richness estimators were used as a measure of γ diversity.

The majority of the techniques used for data analyses are described in Clarke and Warwick (1994) and were implemented using PRIMERv5 (Plymouth Routines in Multivariate Ecological Research) (Clarke and Gorley 2001). True species richness estimators were computed with the EstimateS package (Version 5, Colwell 1997). Statistical analyses were performed using StatView.v5 (SAS Institute Inc. 1998).

Results

Alpha diversity

The number of taxa found at each station varied markedly among the 6 study sites (Fig 2a). The highest median values were calculated for the shallow-water stations in the Weddell (56) and Bellingshausen (44) Seas in the Antarctic, whereas values at deeper stations from the same sites were lower, 36 and 23 respectively. The lowest medians were computed for the Arctic, with a number of 18 and 13 taxa for the deeper and shallower stations, respectively. The post-hoc multiple comparison showed that the number of taxa at the shallow-water stations in the Antarctic was significantly higher than at those in the Arctic. Additionally medians from deeper stations in the Weddell Sea were significantly higher than deeper stations off northeast Greenland.

$E(S_{70})$ also differs noticeably between stations (Fig. 2b). The shallow-water stations in the Bellingshausen Sea showed the widest range (4.17 to 27.35). Highest medians were computed for the Weddell Sea and deeper stations in the Bellingshausen Sea. However, values for shallow

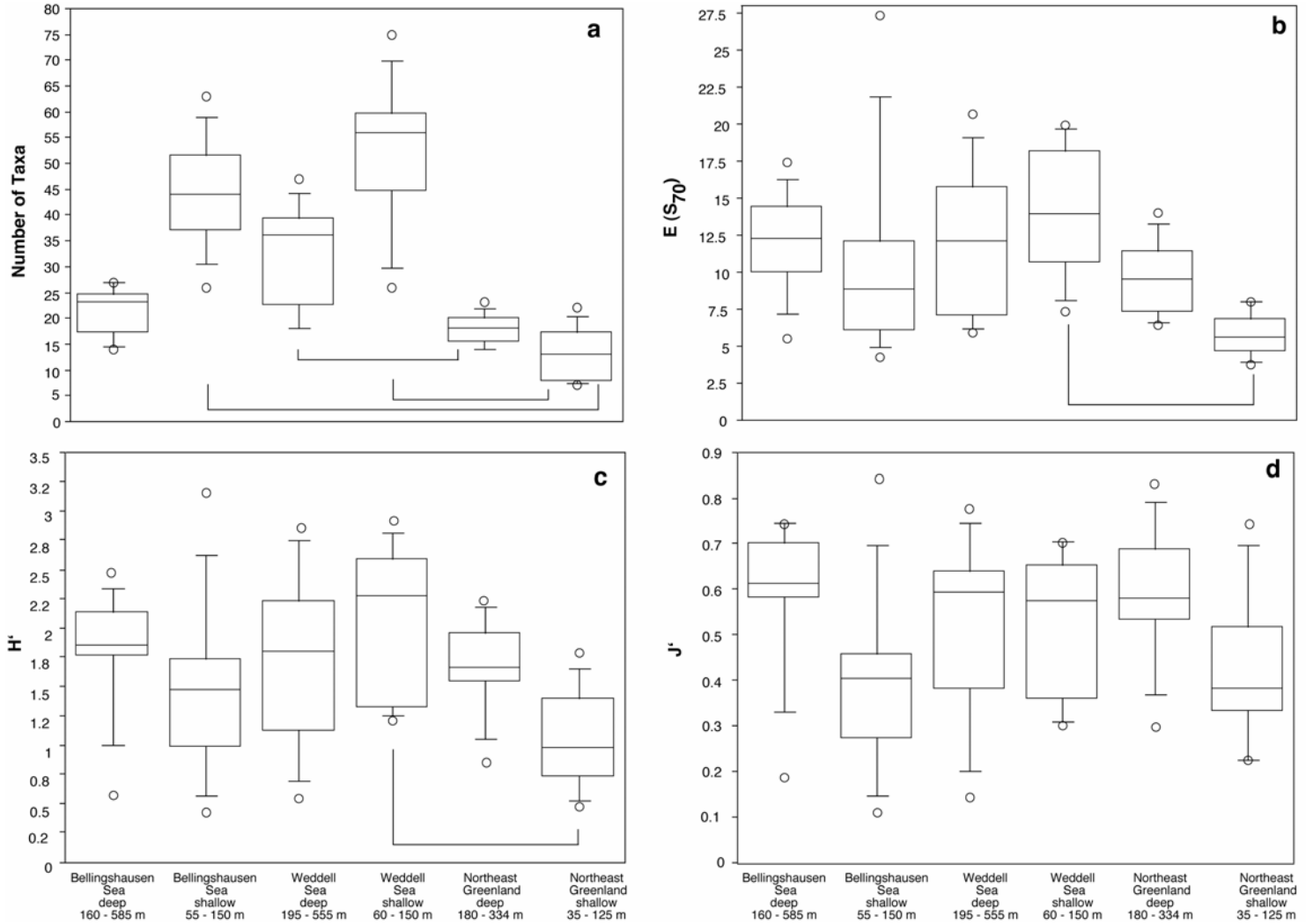

Fig. 2 Within-habitat diversity (α). **(a)** Number of taxa; **(b)** Rarefaction richness estimator E (S70); **(c)** Shannon diversity (H'); **(d)** Pielou's evenness (J') in mega-epibenthic assemblages in Bellingshausen and Weddell seas (Antarctica) and off northeast Greenland (Arctic). Box Plots: the 5 horizontal lines represent 10^{th}, 25^{th}, 50^{th} (median), 75^{th} and 90^{th} percentiles of the variable; circles represent outliers; arrows indicate significant differences (post-hoc multiple comparisons after Nemenyi, $p<0.05$) between investigation sites. Sample size (n)= 9 for each study site

water in the Bellingshausen Sea and deeper stations in the Arctic were similar. The lowest $E(S_{70})$ value was calculated for the shallow-water stations off northeast Greenland. Diversity in the Weddell Sea at shallow stations showed significantly higher values compared to the shallow-water stations in the Arctic.

A similar pattern was discernible for Shannon diversity (H') (Fig. 2c). The Weddell Sea and deeper stations in the Bellingshausen Sea displayed the highest estimates for H'. Again deeper stations off northeast Greenland and shallow-water stations in the Bellingshausen Sea showed similar values for H'. The lowest H' values were calculated for shallow-water stations in the Arctic. However, significant differences in diversity values were only found between shallow-water stations in the Weddell Sea and the Arctic.

The highest median values for Pielou's evenness (J') were observed for the Weddell Sea, deeper stations in the Bellingshausen Sea and the Arctic (Fig. 2d), indicating low dominance at these localities. The lowest J' values and therefore highest dominance, were displayed at shallow sites in the Bellingshausen Sea and shallower stations in the Arctic. No statistical differences were discernible between stations in these cases.

Beta diversity

Whittaker's between habitat diversity displayed a broad range in similarity coefficients within the study sites (Fig. 3). The shallow-water stations from the Arctic showed the widest range (7.8 to 70.3) but also had the lowest median value, indicating a high β diversity. In the Weddell Sea β diversity was high with medians of 35.8 (deep) and 38.4 (shallow), but not as high as in the shallow Arctic (28.3). Deeper stations off northeast Greenland showed by far the lowest β

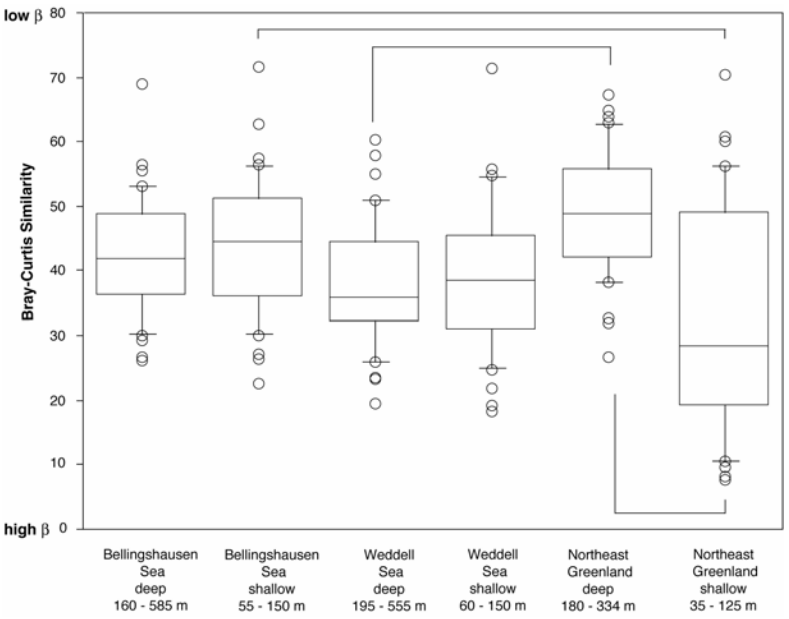

Fig. 3 Between-habitat diversity (β). Distribution of similarity coefficients between all possible combinations of stations (For more details see legend Fig.2). Sample size (n)= 36 for each study site

diversity, with a median value of 48.7. Post-hoc multiple comparison showed that similarities from the shallow-water stations in the Arctic differed significantly from those of the deeper Arctic and shallower Bellingshausen Sea, although not from the Weddell Sea stations. In addition similarity values for the deeper stations off northeast Greenland were significantly higher than the values found in the Weddell Sea, thus indicating a higher species turnover at the latter stations.

Gamma diversity

Values for H' and $E(S_{70})$ showed similar patterns for the regional diversity (Fig. 4a and 4b). The highest mean value was found at the shallow-water stations in the Weddell Sea, followed by mean values from the Arctic and deeper stations in the Bellingshausen Sea. The least diverse sites were shallow stations in the Bellingshausen Sea and deep stations in the Weddell Sea. However, significant differences in diversity values were only found between shallow and deep stations in the Weddell Sea. In addition, highest measures of evenness (J') (Fig. 4c) and therefore lowest dominance were observed at deeper sites in the Arctic and shallow-water stations in the

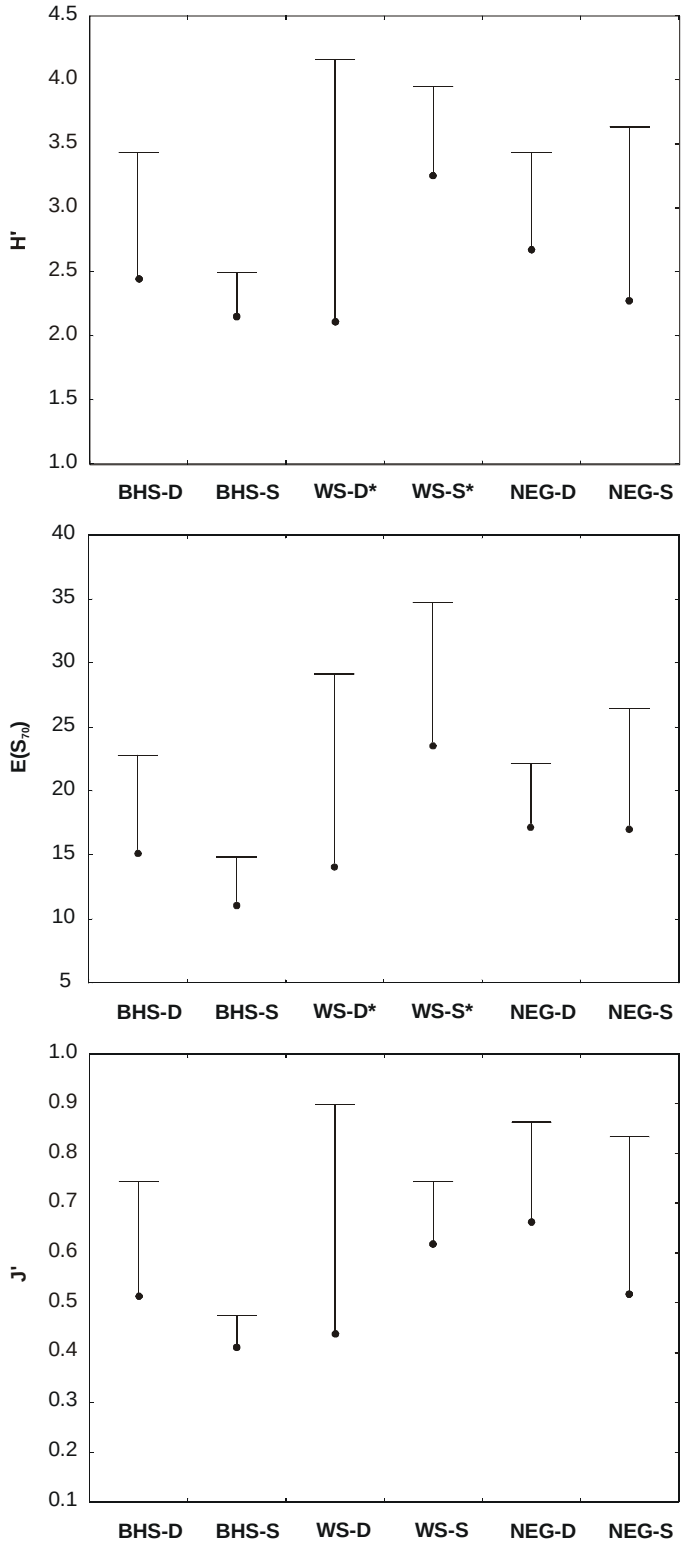

Fig. 4 Regional (γ) diversity. Jack-knife estimates for: a) Shannon diversity (H'); b) Rarefaction richness estimator $E(S_{70})$; c) Pielou's evenness (J') in mega-epibenthic assemblages in Bellingshausen and Weddell Seas (BHS, WS) (Antarctica) and off northeast Greenland (NEG) (Arctic). D: deep stations; S: shallow stations. (For depth details see Fig.2). *: indicates significant differences between investigation sites. Symbols are mean values (n= 9). Bars show SD

Weddell Sea. Shallower stations in the Arctic and deeper sites in the Bellingshausen Sea showed intermediate evenness. The lowest mean values for evenness were found in the Antarctic, at deeper and shallower stations in the Weddell and Bellingshausen Seas, respectively, indicating high dominance in these regions. No statistical differences were discernible between sites.

Mean values of species richness estimators at the Arctic shallow-water stations varied between 50.96 - 105.33 (Fig. 5). At deeper stations off northeast Greenland the range for the different computed estimators was 49.9 – 58.88. Estimators for the Bellingshausen Sea region ranged between 163.88 – 207.31 and

97.2 – 163.25 at shallower and deeper sites, respectively. The Weddell Sea showed a similar pattern, with estimator values for shallower and deeper sites between 161.06 –198.86 and 105.54 – 128.72, respectively.

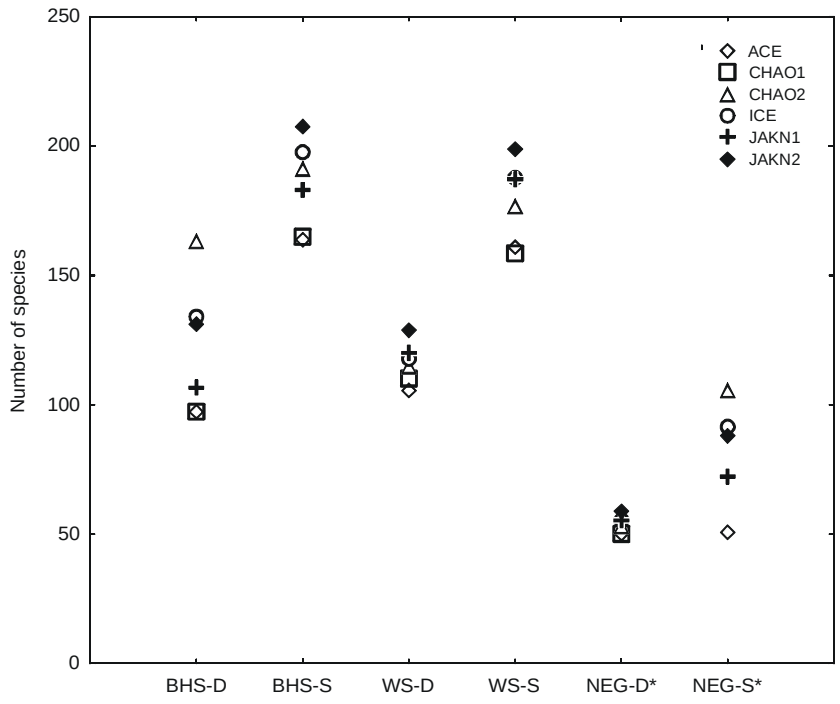

Fig. 5 Regional (γ) diversity. Non-parametric species richness estimators in mega-epibenthic assemblages in Bellingshausen and Weddell Seas (BHS, WS) (Antarctica) and off northeast Greenland (NEG) (Arctic). D: deep stations; S: shallow stations. (For depth details see Fig. 2. *: indicates significant differences between investigation sites. Abundance-based estimators: Chao1 and Abundance-based Coverage Estimator (ACE); Incidence-based estimators: Chao2, Jack-knife 1st order (JAKN1), Jack-knife 2nd order (JAKN2) and Incidence-based Coverage Estimator (ICE). Symbols are mean values (n= 9). For all calculations involving random orderings of the samples, 50 randomisations (without replacement) were used. Estimators were calculated using EstimateS package (V.5, Colwell 1997)

The highest mean values for the data set of true species richness estimators were calculated for the Southern Ocean (Fig. 5). However, these values were higher at the shallow-water stations of the Antarctic sites investigated. Also in the Arctic, shallower stations displayed higher estimator ranges than deeper ones. Significant differences in diversity values were only found between deep and shallow-water sites off northeast Greenland.

Discussion

Measures of species diversity are central to many aspects of ecology and conservation (Whittaker 1960, Magurran 1988, Gaston 1996, Gray 2000). The concept of biological diversity as the "variety of living organisms" cannot be summarized by a single measure (May 1994, Ellingsen 2001) and there is also no single correct scale at which to view ecosystems (Levin 1992). The concept of diversity expresses something more than the notion of the effective number of species present (Hill 1973, Williamson 1997). Distributions of species and community differences should be taken into account in addition to species diversity when measuring marine biodiversity (Ellingsen 2001).

Consequently it is not surprising that the results presented here are complex and that they confirm the statement made in the Introduction that detailed knowledge is necessary to come to reliable generalizations on biodiversity patterns. Additionally, the results demonstrate that the more details are known the more expected generalities become unclear even if modern analytical methods are applied. Due to this difficulty hypotheses and results are presented in an overview in Table 1, in which the comparisons between the Arctic and the Antarctic as well as shallow and deep polar samples at different spatial scales are shown diagrammatically. Here only significances between comparable units are depicted, e.g. between shallow and deep assemblages within one investigation site or between shallow sites but not for example between shallow Antarctic and deep Arctic stations or vice versa.

Since most results are related to each other classifications in terms of spatial scales or depth strata represent rather gradients than discrete differences. As a consequence, the discussion is not only structured according to the hypotheses stated in the Introduction and to spatial scales but also to the two general driving forces behind biodiversity patterns, evolution and ecology.

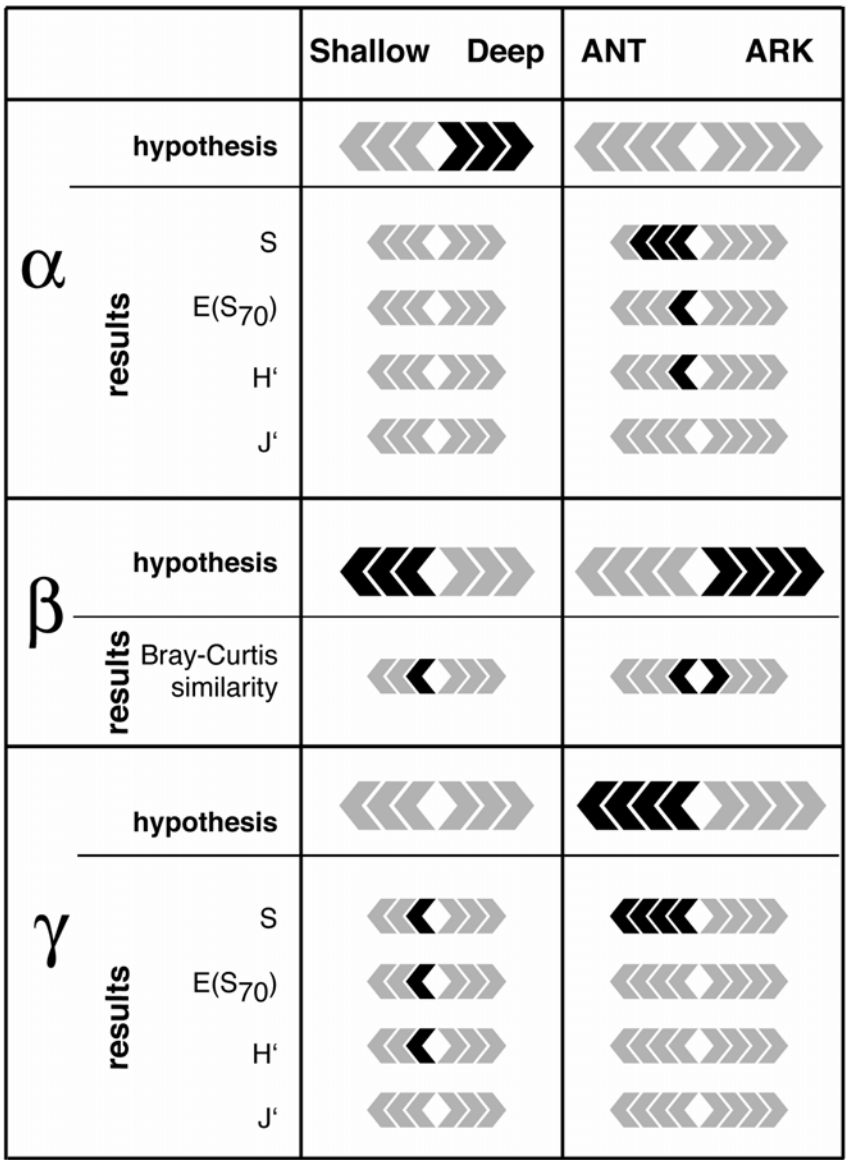

Table 1 Schematic representation of the results and hypotheses tested for within-habitat (α), between-habitat (β) and regional (γ) diversity at shallow (35-150 m) and deep (160-585 m) sites and for Antarctic (ANT) and Arctic (ARK) regions. For details of the hypotheses see introduction. S number of taxa; E (S_{70}): rarefaction richness estimator; H': Shannon diversity; J': Pielou's evenness. The tone intensity of the arrows indicates the trend of the direction into which the hypothesis goes.

Gamma and beta diversity

Diversity, often reduced to pure species numbers, is regulated at the regional (gamma) scale mainly by historical processes (Crame and Clarke 1997, Gray 1997). Consequently, dissimilarities in the evolution of Arctic and Antarctic faunas (Dayton 1990) have to be considered, when trying to understand patterns we observe today (Clarke 1996b). Environmental stability over evolutionary time was identified by Sanders (1969) as the main driver to foster specialization e.g. in the deep sea since species are able to adapt to each other and require less effort to adapt to the environment. The resulting effect is that many species with narrow, almost non-overlapping niches coexist (Grassle and Sanders, 1973). In this convincing concept, however, the role of large, primarily geomorphological disturbances is ignored. Pianka (1978) also considered competition as an important evolutionary force that has led to niche separation, specialization and diversification. In addition, Dayton and Hessler (1972) pointed out the importance of continued biogenic disturbance as a significant factor in maintaining high diversity. They argued that as an effect of disturbance, resources might become less limiting and as a result the probability of competitive exclusion is reduced.

Our results show that both Antarctic study sites are richer in the number of mega-epibenthic taxa than the Arctic. This cannot be explained exclusively by either stability or disturbance. An increase in species number as a result of environmental stability during discrete periods such as interglacials and glacials according to Sanders (1969) was regularly and irregularly interrupted by climatic shifts with enormous consequences for the benthos (Clarke and Crame 1989). In this context vicariance can have a great importance (Clarke and Crame 1992), since speciation may occur as a result of geographic or ecological separation and subsequent isolation of portions of an

original population (Pielou 1979, Barton 1990, Myers and Giller 1990). The rate of resulting speciation may vary systematically with conditions that promote reproductive isolation between populations and that enhance the rate of evolution (Ricklefs 1987).

However, both polar regions generally experienced the same conditions. One major difference in this context might be the fact that in case of large-scale marine warming and cooling the Arctic fauna had a chance to migrate longitudinally, and consequently genetic exchange among populations was not blocked as much as in the Antarctic by large ice extensions. We do not claim for a complete knowledge of all evolutionary relevant factors but it seems to be logical that their characteristic combination and specific details may have led to the higher species number in the Antarctic. This includes not only environmental conditions but also positive and negative interspecific interactions, such as development of commensalism, e.g. epibiotic life (Gutt and Schickan 1998) as well as well balanced concurrence and competition (Dayton et al. 1974). In addition the Arctic is younger as a cold environment, what could probably explain its lower species richness since there may have not been enough time and environmental stability (Grassle and Sanders, 1973) for the establishment of an extensive species component (Gray 2001). Indeed different authors (Vermeij 1991, Dunton 1992) have remarked that the Arctic marine ecosystem is in an evolutionary sense still facing colonization.

Not many theories exist about evolutionary processes triggering a high numerical equitability among species or, alternatively, a high dominance of single species. Our results show that at a large spatial scale species numbers are not related to dominance patterns; otherwise any of the variables including equitability, $E(S_{70})$, H', or J' would also be higher in the Antarctic. Obviously the above-mentioned complexity of forces does not lead to a composition of species with a higher

numerical equilibrium. In the older Antarctic as well as in the younger Arctic communities (Knox and Lowry 1977, Dayton 1990, Gray 2001) both, rare and dominant species seem to perform independently a successful adaptive strategy over evolutionarily relevant periods.

To compare the faunas of shallower and deeper shelves in the light of evolutionary processes is only worthwhile if a clear depth zonation exists as found in the Arctic (Piepenburg and Schmid 1996). In the Antarctic except for a zone exposed to permanent sea-ice disturbance a large proportion of the fauna is eurybathic (Brey et al. 1996). In addition, also a true shallow-water fauna exists (Gutt 1991). Generally, it can be stated that over both evolutionarily and ecologically relevant time scales the environment in shallow-water systems is more heterogeneous and dynamic than in deeper systems, an assumption on which some of our hypotheses were based. In the Arctic the deeper site was slightly poorer in species and species turnover (beta-diversity) indicating a lower habitat heterogeneity compared to shallower habitats. In the Arctic only the shallow depth stratum is affected by iceberg scouring. Consequently, the difference between shallow and deeper sites can reflect among other locally changing ecological conditions this specific impact. However, it is not yet quantitatively investigated at this study site.

In the Antarctic all regional species numbers in the shallow sites were higher than in deeper ones including one significant difference, but in contrast to the Arctic this cannot be explained by a higher species turnover. This might indicate a different origin or colonization history of shallow and eurybathic species. At the deeper stations a high proportion of eurybathic species occurs as well as in the shallow sites where, however, additional species restricted to shallow waters are present. The deeper species could colonize the circumpolar continental slope during ice ages.

The shelf, however, was mainly covered by overlying shelf ice (Anderson et al. 1980, Anderson 1991, Harris and O'Brien 1996) and many populations, species, and their assemblages restricted to shallow water were separated and evolved during these periods in sparse Antarctic shallow water refuges. At the beginning of interglacials these mixed among each other and with the deeper species on the continental shelf primarily without much competition and, thus, contributed to the high regional species richness

Concerning the comparisons between species turnover (beta diversity) in the Arctic and Antarctic samples no systematic trends were found since in one case the Arctic and in another the Antarctic study site had a significantly higher species turnover. As with the comparison between depth strata this indicates that rather locally changing ecological conditions within the study sites than differences in long-term evolutionary processes between both polar regions affect species turnover patterns.

Alpha diversity

Why did the results from both comparisons Arctic versus Antarctic, shallow versus deep not follow our hypotheses? We cannot imagine that recent ecological conditions in small areas of 100 m^2 or, in other words, the carrying capacity for alpha diversity differ in a way that the presence of more species is favoured in one of the two polar regions by the presence of a higher number of microniches. Generally, small-scale coexistence of many species is also supported by a fast dispersal through reproductive stages (Holmes and Wilson 1998, Amarasekare and Nisbet 2001, Shurin and Allen 2001). However, despite the fact that recently for some abundant species

meroplanktonic larvae have been discovered (Pearse et al. 1991, Stanwell-Smith et al. 1999, Gambi et al. 2000b, 2001), environmental conditions in the Antarctic seem to favour direct development (Poulin et al. 2002). Nevertheless, at the local spatial scale species numbers were higher in the Antarctic. We believe that this is due to the clearly higher regional diversity. This includes the occupation of specific small-scale niches, which, however, must be primarily considered as a large-scale phenomenon. Such adaptive strategies evolved in the entire Antarctic as the above mentioned epibiotic life or any traits in the early life history e.g. preference of generally poorly sorted sediments which are so far totally undiscovered.

The only clear gradient following Hill's concept of a changing relevance of species numbers and equitability confirms the interpretation that the regionally high species richness is the main reason for the high local species numbers. If local environmental conditions would have a major effect also equitability results would differ between Arctic and Antarctic study sites.

Another reason for the higher local species numbers in the Antarctic could be differences in natural disturbances such as predation pressure or iceberg scouring (Lewis and Blasco 1990, Gutt 2000, Gutt and Starmans 2001). If in the Antarctic most, if not all, sites investigated did not return to an advanced stage of equilibrium they could harbour a maximum diversity according to the intermediate disturbance hypothesis (Huston 1979). The impact of iceberg scouring on polar benthic communities can play an important role in both hemispheres (Gutt et al. 1996, Conlan et al. 1998, Gutt 2001), however, studies focussing on smaller spatial scales are, at least for the Antarctic, necessary to detect corresponding effects (Gutt and Piepenburg 2003). If the intermediate disturbance hypothesis can be applied the question remains open, whether in the Arctic disturbances are less frequent or more effective and thus species numbers are reduced. In

the latter case we would expect also a higher evenness in the Arctic, which we did not find. It is also still open whether the Antarctic benthos is still in a non-mature stage after the last glaciation (Gutt 2000) and whether in the future due to competition less robust species will get extinct at least at the local scale.

In general we conclude that at the level of the here presented metaanalysis many ecological processes are superimposed and generate even among the relatively simple diversity parameters a complexity, which does not allow for many generalizations. Maybe studies with more detailed questions and focussing on more specific temporal and spatial scales or specific groups of animals will in fact not answer the "big" questions but can provide more clear insight in driving forces behind polar benthic biodiversity patterns.

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- Marie von Ebner-Eschenbach -

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8 Appendices

8.1 List of abbreviations

Abbreviation	Description
ACE	Abundance-based Coverage Estimator
ANOSIM	Analysis of similarities
cm	Centimetre
EASIZ	Ecology of the Antarctic Sea Ice Zone
H’	Shannon-Wiener Index
ICE	Incidence-based Coverage Estimator
IMS	Index of multivariate seriation
J’	Pielou’s evenness
km	Kilometre
m	Metre
m^2	Square metre
MDS	Non-metric multidimensional scaling
ROV	Remotely Operated Vehicle
S	Number of taxa
SIMPER	Similarity percentages
Stn	Station

8.2 List of ROV stations

Table 1 Video transects undertaken from the British Antarctic Survey research vessel R.R.S. "James Clark Ross" in the Bellingshausen Sea (northern Marguerite Bay). *Exp* expedition; *TL* Transect length; *AI* Adelaide Island; *HI* Horseshoe Island; *MI* Millerand Island

Exp	Stn	Date	Position (start)		Position (end)		Time	Depth	TL	Area
			Lat (S)	Long(W)	Lat (S)	Long(W)		(m)	(m)	
JR37	002	03.12.1998	67°35'53.96''	68°13'31.55''	67°35'59.85''	68°13'44.74''	21:29 – 22:05	72-132	257	AI
JR37	005	04.12.1998	67°48'39.39''	67°20'47.53''	67°48'28.09''	67°20'07.34''	20:29 – 21:59	77-68	788	HI
JR37	006	05.12.1998	67°48'37.95''	67°20'39.95''	67°48'30.83''	67°20'20.22''	11:35 – 12:28	70-72	386	HI
JR37	010	06.12.1998	68°10'10.08''	67°21'02.32''	68°10'04.86''	67°21'33.67''	12:22 – 13:30	68-71	504	MI
JR37	011	06.12.1998	68°10'44.61''	67°10'56.15''	68°10'44.89''	67°11'01.24''	15:46 – 16:27	143-135	425	MI
JR37	012	07.12.1998	67°49'05.73''	68°41'13.81''	67°49'11.79''	68°41'43.93''	13:30 – 14:36	112-97	451	AI
JR37	014	07.12.1998	67°44'59.08''	68°27'06.19''	67°45'02.63''	68°27'38.57''	19:56 – 21:00	71-56	437	AI
JR37	015	08.12.1998	67°35'57.66''	68°13'28.49''	67°36'04.43''	68°13'44.87''	11:53 – 13:02	90-208	396	AI

Table 2 Video transects undertaken from the Alfred-Wegener Institute research vessel "Polarstern" in the Weddell Sea. *Exp* expedition; *TL* Transect length; *KN* Kapp Norvegia; *AB* Atka Bay

Exp ANT	Stn	Date	Position (start)		Position (end)		Time	Depth	TL	Area
			Lat (S)	Long(W)	Lat (S)	Long(W)		(m)	(m)	
XIII/3	024 IIA	21.02.1996	71°07'19.68''	11°26'47.16''	71°07'20.62''	11°28'22.85''	11:26 – 12:39	144-62	1358	KN
XIII/3	024 IIB	21.02.1996	71°07'22.80''	11°28'40.80''	71°07'33.60''	11°29'24''	12:53 – 13:44	109-112	865	KN
XIII/3	032 II	04.03.1996	70°31'28.43''	08°30'46.31''	70°32'02.35''	08°34'16.70''	02:35 – 03:51	145-131	2473	AB
XIII/3	032 IV	05.03.1996	70°32'28.52''	08°36'04.77''	70°31'42.88''	08°36'19.90''	01:39 – 02:54	132-139	1466	AB
XV/3	281	01.03.1998	70°40'15.31''	08°01'35.12''	70°40'00.29''	08°02'25.74''	19:00 – 20:07	64-66	771	AB
XVII/3	059-1	30.03.2000	70°40'25.72''	07°41'08.63''	70°40'18.84''	07°40'38.96''	02:09 – 03:11	126-101	433	AB
XVII/3	111-1	05.04.2000	71°07'33.85''	11°27'59.98''	71°07'32.27''	11°27'38.88''	00:48 – 01:16	89-61	300	KN

8.3 Tables of abundance of taxa

Table 1 Abundance of taxa (n/100m^2) per station in the Marguerite Bay (Bellingshausen Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8.4).

Taxa	Station							
	002	**005**	**006**	**010**	**011**	**012**	**014**	**015**
RRC	26,6	36,7	0,0	0,6	10,8	0,0	1,6	1,4
RSY	3,5	1,1	0,0	0,0	2,5	0,0	7,8	0,7
RRbt	751,2	2730,0	2444,2	188,9	0,0	6,0	0,0	972,6
DEM	113,2	155,4	103,6	45,9	20,9	26,6	14,6	59,2
DEMsp12	0,0	0,0	0,0	5,2	1,7	0,0	0,0	2,2
DEMsp13	46,2	0,6	2,1	6,9	5,8	0,0	1,4	12,3
CAL	3,5	0,0	2,1	0,0	0,0	0,0	0,0	0,0
CIA	11,6	4,5	5,7	4,2	4,2	0,0	0,5	1,4
CIB	13,9	3,4	4,3	2,3	0,0	0,5	1,6	2,2
CTN	0,0	0,0	0,0	0,0	0,0	0,0	0,0	8,7
CTH	2,3	0,0	2,1	1,7	2,5	0,0	0,0	0,0
HAL	4,6	0,6	0,0	0,6	1,7	3,8	16,1	1,4
HALsp1	0,0	0,0	5,0	0,0	0,0	0,0	0,0	0,0
HALsp7	0,0	0,0	0,7	0,0	0,0	0,0	0,0	0,7
HNA	4,6	4,0	3,5	0,0	0,0	0,5	0,0	2,9
HNAsp1	3,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0
ISO	1,2	1,1	0,0	0,0	0,0	0,5	0,0	0,0
ISOsp3	1,2	0,0	0,0	0,0	0,0	0,0	0,0	0,7
LAP	0,0	0,0	0,7	0,0	0,8	0,0	0,0	0,0
LAT	1,2	0,6	0,0	0,0	0,8	1,6	0,0	0,0
LATsp1	0,0	0,0	0,0	0,0	0,0	0,5	0,0	4,3
LAV	0,0	0,0	0,0	0,0	0,0	0,5	0,0	0,0
MYC	1,2	15,3	5,7	0,0	4,2	0,0	1,6	2,2
PHO	0,0	36,2	0,0	0,0	0,0	0,0	0,0	0,0
PII	1,2	0,6	0,7	6,3	0,0	0,0	0,0	0,0
PIN	4,6	1,1	0,0	2,3	0,0	0,5	0,0	0,0
SBL	0,0	0,0	0,0	0,0	0,0	0,0	0,0	2,9
SBR	6,9	1,7	1,4	1,7	2,5	23,3	7,8	3,6
TED	0,0	9,4	5,7	4,2	2,5	0,0	1,6	0,0
TEO	0,0	0,0	0,0	1,1	0,0	0,0	0,0	0,0
TEL	1,2	4,5	5,7	63,2	2,5	11,4	1,6	0,7
TEV	3,5	0,0	0,0	0,0	0,0	0,5	0,0	0,0
YEB	4,6	22,7	104,3	28,1	0,0	0,0	89,5	0,0
FSH	1,2	2,3	3,5	1,1	21,7	1,3	2,9	2,2
HYD	120,2	40,7	55,3	64,9	78,5	274,1	48,9	55,6
HYDsp3	0,0	0,0	0,0	0,0	0,0	8,1	0,0	0,0
OSA	0,0	0,0	0,0	0,0	0,0	0,5	34,3	0,0
SYM	0,0	0,6	0,0	0,0	0,0	0,0	0,0	0,0
LUC	0,0	0,0	0,0	0,0	0,0	12,5	0,5	0,0
ANT	9,2	6,8	0,7	1,1	0,0	0,0	0,0	4,3
ALY	0,0	0,0	0,0	0,0	2,5	2,7	36,9	0,0
ALYsp5	0,0	0,0	0,0	0,0	0,0	0,0	4,7	0,0
ALM	1,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0
GER	0,0	0,0	0,0	0,6	0,0	0,0	0,0	0,0
GOR	0,0	11,3	0,0	0,0	3,3	1,6	0,5	0,0
ARN	0,0	2,3	1,4	0,6	0,0	0,0	6,2	0,0
DAS	9,2	0,0	0,0	4,6	0,0	28,8	2,6	5,6

Table 1 [continued] Abundance of taxa (n/100m^2) per station in the Marguerite Bay (Bellingshausen Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4).

Taxa	Station							
	002	**005**	**006**	**010**	**011**	**012**	**014**	**015**
ISI	2,3	0,0	0,0	0,0	7,5	6,0	0,5	0,0
PREsp1	79,7	14,7	15,6	102,8	12,5	5,4	50,5	115,6
PREsp2	11,6	102,3	132,7	57,4	1,7	15,3	9,9	1,4
PRI	4,4	0,0	1,4	8,6	3,3	45,6	2,9	19,6
THO	19,6	6,8	1,4	28,1	20,0	124,3	47,3	19,6
FAN	0,0	1,7	2,8	2,9	0,0	2,2	0,0	0,0
IDI	0,0	0,0	0,0	0,0	0,0	0,5	0,0	2,9
ACT	5,8	1,7	3,5	14,9	0,0	0,5	5,2	0,0
ACTsp3	4,6	0,0	0,0	0,0	0,0	0,0	0,0	2,9
ACTsp6	1,2	0,0	0,0	0,0	0,0	0,0	0,0	1,4
ACTsp8	13,9	0,0	0,0	0,0	0,0	0,0	0,0	6,5
ACTsp9	2,3	0,0	0,0	0,0	0,0	0,0	0,0	2,2
ACTsp13	12,8	0,0	1,4	3,4	0,0	0,0	11,4	2,2
ACTsp19	0,0	0,0	0,0	0,0	0,0	0,0	0,0	3,6
ACTsp20	83,2	0,0	0,0	0,0	0,0	0,0	0,0	34,0
COF	1,2	1,7	0,0	0,0	0,0	0,0	5,2	1,4
ICY	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,0
CER	69,3	1,7	13,5	13,3	50,9	1,9	2,3	2,2
CERsp5	16,2	0,6	0,0	0,0	0,0	0,0	0,0	57,8
NEM	8,9	1,7	4,3	0,6	0,0	1,6	1,9	4,3
BUC	0,0	0,0	0,7	1,1	0,0	0,0	0,0	0,7
NUM	0,0	1,1	0,0	0,0	0,0	1,9	0,0	0,0
NEO	0,0	0,0	3,5	0,0	0,0	0,0	0,5	0,7
HAR	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,0
NUD	0,0	0,0	2,8	0,0	0,0	0,0	0,0	0,0
RIS	3,5	0,0	0,0	0,0	0,0	0,0	1,4	0,0
POL	0,0	0,0	0,0	0,0	0,0	0,0	6,2	0,0
PTA	4,6	0,0	0,0	0,0	0,8	0,0	0,0	0,0
SAB	0,0	5,7	5,7	2,3	9,2	356,6	11,4	0,0
SABsp4	0,0	0,0	1,4	1,1	0,8	0,5	0,0	1,4
SABsp5	34,7	0,0	1,4	0,0	1,7	2,2	27,1	3,6
SABsp11	0,0	0,0	0,0	0,0	0,0	6,5	1,6	0,0
SABsp12	0,0	0,0	0,0	0,0	0,0	1,6	0,5	0,7
POS	0,0	1,7	7,1	7,5	9,2	0,0	71,3	0,0
POSsp1	1,4	0,0	0,0	4,2	15,0	917,6	2,6	6,5
POSsp2	0,0	0,0	0,0	2,9	0,0	0,0	0,0	0,0
PYC	0,0	0,0	0,0	1,1	0,0	2,7	0,5	0,0
GLY	0,0	0,0	0,0	0,0	0,0	1,9	0,5	0,0
HEMsp2	0,0	0,0	0,0	0,6	0,8	0,0	0,0	0,0
HEMsp3	0,0	0,0	0,7	0,0	0,0	0,0	0,0	0,0
ASC	0,0	3,4	0,0	1,7	0,8	7,6	3,6	0,0
MOP	42,7	6,8	18,4	1,7	4,2	14,7	6,2	34,7
CNV	9,2	44,7	51,1	1,7	6,7	0,0	5,5	5,6
PYU	0,0	16,4	0,0	0,0	0,0	0,5	0,0	0,0
PYB	2,3	0,0	0,0	1,1	2,5	17,4	1,6	7,2
PYD	67,1	0,0	38,3	7,5	0,0	2,7	1,4	2,2
PYS	25,4	0,0	0,0	0,0	2,5	3,3	0,0	14,5
SYA	0,0	0,0	2,1	0,0	0,0	0,0	0,0	0,0
SCY	22,0	7,3	0,0	12,6	3,3	8,7	12,0	2,2
APLsp2	0,0	0,0	0,0	0,0	0,0	0,0	0,5	0,0

Table 1 [continued] Abundance of taxa (n/100m^2) per station in the Marguerite Bay (Bellingshausen Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4).

Taxa	Stations							
	002	**005**	**006**	**010**	**011**	**012**	**014**	**015**
APLsp3	0,0	0,0	0,0	0,0	0,0	0,0	1,4	0,0
TON	3,5	1,1	0,0	0,0	0,0	0,0	0,0	0,7
SYN	0,0	0,0	0,7	1,1	0,0	1,9	4,7	0,0
SYNsp31	0,0	0,0	0,0	0,0	0,0	0,0	1,4	0,0
ASG	0,0	0,6	0,0	0,0	0,0	11,4	0,0	0,0
AST	18,5	18,9	13,5	8,6	3,3	21,2	17,2	2,9
ASTsp25	0,0	0,0	0,0	0,0	0,8	0,0	3,6	0,0
ACO	5,8	9,7	3,5	0,6	0,8	1,6	2,6	0,7
CUE	0,0	0,0	0,0	0,0	0,0	0,5	0,0	0,0
HEN	3,5	0,0	6,4	2,9	0,8	0,5	1,4	1,4
MAC	4,6	11,9	20,6	4,2	2,5	4,3	6,8	2,2
ODO	0,0	9,7	5,0	2,9	0,0	2,2	1,9	0,7
POR	0,0	2,3	0,7	1,1	0,0	4,3	0,0	0,0
OPH	3923,7	3856,4	4574,8	3766,4	923,1	657,3	2589,2	2464,6
OGI	0,0	4,0	0,7	0,0	0,0	0,0	2,6	0,0
CID	0,0	0,0	0,7	0,0	0,0	1,6	0,0	0,0
STE	1653,4	1656,7	1857,5	884,2	32,5	29,3	54,7	654,7
HOL	3,5	4,0	0,7	0,0	5,0	3,3	0,5	1,4
HOLsp10	27,7	0,0	0,0	0,0	0,0	0,0	0,0	0,0
HOLsp11	0,0	0,0	0,0	0,0	0,0	9,2	0,0	0,0
DEN	2,3	0,6	1,4	1,7	10,0	34,2	214,9	1,4
DENsp2	1,2	0,0	0,0	0,0	0,0	4,3	0,0	0,0
EKM	16,2	0,6	0,7	0,0	0,0	0,5	9,9	2,9
PSO	0,0	0,0	0,0	0,0	0,0	1,9	1,4	0,0
CRI	5,8	0,0	0,0	0,0	3,3	638,9	5,2	0,7
BRY	1,2	2,8	3,5	1,1	2,5	1,9	5,2	0,7
BRYsp7	0,0	0,0	0,7	0,0	0,8	0,0	0,0	0,0
ALC	0,0	4,0	0,0	0,0	0,0	0,0	0,0	0,0
AUS	0,0	0,6	0,7	0,6	0,0	1,9	0,0	0,0
BOD	0,0	1,7	2,8	1,1	0,0	1,9	0,5	0,0
CAR	0,0	0,0	0,0	0,0	0,8	0,5	0,0	0,0
CAT	2,3	1,7	0,0	2,3	3,3	0,5	0,0	0,7
CEL	0,0	5,7	0,0	0,0	0,0	1,6	0,0	0,0
CHO	0,0	0,0	0,0	0,0	0,8	2,2	0,0	0,0
CLN	1,2	0,6	0,0	0,0	1,7	0,5	0,0	0,7
CYCsp1	2,3	0,0	0,0	0,0	0,0	0,0	0,0	0,0
FAS	0,0	1,7	0,0	2,9	0,8	1,9	1,4	0,0
FLU	1,2	0,0	0,0	0,0	1,7	1,9	2,6	0,7
FLUsp2	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,0
KYM	0,0	0,0	0,0	0,0	0,8	0,5	0,0	0,0
LAG	0,0	0,0	0,0	0,0	0,8	1,6	0,0	0,0
MEO	0,0	0,0	0,0	0,0	0,8	2,2	0,0	0,0
ORT	0,0	0,0	0,0	0,0	0,0	14,7	0,0	0,0
RET	2,3	0,0	0,0	0,6	0,8	0,5	0,5	0,0
BSH	0,0	0,6	0,0	2,9	3,3	1,6	2,6	0,0
PISsp2	0,0	0,0	0,0	3,4	0,0	0,0	0,0	0,0
PAG	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,0
TRE	9,2	5,9	2,8	0,6	0,8	0,5	0,0	1,4

Table 2 Abundance of taxa (n/100m^2) per station in the Four Seasons Bank (Weddell Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4). *S*: shallow; *M*: middle; *D*:deep.

Taxa	Stations				
	111-1	**24IIA-S**	**24IIA-M**	**24IIA-D**	**24II-B**
RRC	1,8	0,0	0,0	0,0	8,6
RSY	0,9	3,2	1,0	12,2	23,7
RRbt	0,0	0,0	0,0	0,0	9,7
DEM	145,9	79,1	56,2	34,4	23,2
CAL	0,0	1,2	4,9	0,0	1,8
CIA	4,4	0,0	0,5	1,7	5,9
CIB	69,4	5,7	58,2	232,1	1557,5
CTH	0,9	0,0	0,0	1,1	0,0
HAL	17,6	10,9	107,0	175,4	0,5
HALsp7	15,8	0,0	0,0	0,0	0,0
HALsp11	0,0	3,6	24,4	3,9	0,0
HNA	7,3	0,0	0,5	2,8	348,0
HNAsp1	4,4	0,0	2,0	0,6	7,6
HOM	72,6	149,4	297,7	1,7	0,0
HOMr	35,1	0,0	0,0	0,0	0,0
IOP	2,6	0,0	3,4	4,4	71,8
ISO	2,6	0,0	0,0	0,6	0,0
ISOsp1	0,0	0,0	0,5	1,1	0,0
ISOsp2	2,6	2,0	2,4	0,0	1,8
ISOsp3	4,4	0,0	0,0	1,1	23,2
LAP	1,8	0,0	0,0	0,0	0,0
LAV	0,0	0,4	0,5	1,1	0,0
MOL	0,0	0,0	0,0	0,6	46,4
MYC	0,0	0,0	0,0	0,6	0,0
PII	66,8	25,8	0,0	0,6	9,2
PIN	26,4	5,7	0,0	0,0	5,9
POC	0,0	0,0	0,0	0,0	9,2
SBL	2,6	71,5	50,8	11,7	27,5
SBR	6,2	0,0	10,3	86,6	7,7
TED	0,0	0,0	106,6	188,8	52,9
TEL	1,8	0,8	1,5	3,3	0,5
TEV	1,8	0,0	0,0	0,0	0,0
TEN	2,6	0,0	0,0	0,0	0,0
YEB	1,8	0,0	1,0	121,0	0,0
FSH	0,0	0,0	8,3	7,2	2,7
HYD	213,5	16,1	37,1	44,4	62,0
HYDsp1	22,0	0,0	0,0	0,0	0,0
HYDsp2	0,0	0,0	0,5	0,0	0,0
HYDsp4	15,8	0,0	0,0	0,0	0,0
HYDsp5	0,0	19,8	0,0	0,0	76,1
HYDsp6	14,9	0,0	0,0	0,0	0,0
HYDsp8	254,0	0,0	0,0	18,9	0,5
COM	257,5	0,0	0,0	0,0	0,0
COP	185,4	11,7	0,0	3,3	1,8
COR	8,0	0,0	0,0	1,7	0,5
DRO	14,6	0,0	0,0	0,0	0,0
OSA	37,6	337,5	179,9	182,7	17,8
SCH	54,5	213,6	478,5	24,4	43,7
SCHsp2	171,4	0,0	0,0	0,0	0,0
SYM	0,9	66,6	33,2	12,2	0,0

Table 2 [continued] Abundance of taxa (n/100m^2) per station in the Four Seasons Bank (Weddell Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4). *S*: shallow; *M*: middle; *D*:deep.

Taxa	Stations				
	111-1	**24IIA-S**	**24IIA-M**	**24IIA-D**	**24II-B**
TUB	0,0	8938,6	5,9	0,0	59,9
ANT	0,9	4,8	0,5	7,8	4,9
CLA	283,0	1052,5	151,0	0,6	0,0
ALY	17,6	4,4	1,0	0,6	0,5
ALYsp5	0,9	0,0	0,0	0,0	0,0
ALM	17,6	59,7	6,4	10,0	0,5
GER	1,8	0,0	3,9	0,0	0,0
GOR	58,9	0,0	11,7	2,8	1,8
GORsp11	0,0	0,0	17,1	28,9	1,6
AIN	95,8	0,0	0,5	2,8	0,0
ARN	97,5	416,2	1406,3	184,9	9,2
DAS	4,4	0,0	2,0	16,7	0,0
PREsp1	65,9	26,6	85,5	9,4	32,4
PREsp2	23,7	2,4	20,0	89,9	0,5
PRI	0,0	1,2	159,8	159,3	127,3
THO	1,5	0,0	97,3	206,5	9,7
FAN	35,1	3,2	0,0	0,6	1,6
IDI	0,0	0,0	0,0	0,0	2,7
POG	0,0	90,4	0,0	0,0	0,0
ACT	1,8	1,2	2,4	6,1	0,0
ACTsp3	0,0	0,0	0,0	0,0	0,5
ACTsp6	0,0	0,0	0,0	0,0	0,5
ACTsp8	0,0	0,8	1,0	5,0	1,6
EDW	4,4	0,0	0,0	0,0	1,8
HOR	2,6	1,2	1,0	4,4	0,5
COF	0,0	0,0	0,0	0,0	0,5
CER	6,2	4,0	0,0	5,6	0,0
NEM	4,4	1,2	0,0	0,0	0,0
NUD	57,1	7,3	0,5	2,2	0,0
RIS	1,8	0,0	0,0	0,0	0,0
SAB	21,1	5,2	83,1	83,3	1,1
SABsp3	0,0	0,0	0,0	0,0	9,7
SABsp4	0,0	0,0	0,0	0,0	0,5
SABsp5	78,2	0,0	0,0	0,0	148,4
SABsp7	0,0	0,0	0,0	1,1	0,0
SABsp12	29,0	0,0	0,0	0,0	0,5
POS	0,0	0,0	0,0	5,6	0,0
POSsp1	89,6	101,3	100,7	20,5	3,2
PYC	66,8	39,2	18,6	7,2	8,9
GLY	0,9	0,0	0,0	0,0	1,6
HEMsp3	1,8	0,0	0,0	0,0	0,0
ASC	0,9	0,0	2,0	0,6	0,0
MOP	0,9	0,0	0,5	0,0	2,2
CNV	0,9	0,8	0,0	0,6	1,8
PYU	0,0	0,4	0,5	0,0	0,0
PYS	0,0	0,0	0,5	0,0	0,0
SYA	0,0	0,0	0,0	6,1	8,6
SCY	1,8	0,0	0,0	0,0	0,0
APLsp2	0,0	0,0	0,0	0,6	2,7
APLsp3	0,9	0,0	1,0	2,2	2,2

Table 2 [continued] Abundance of taxa (n/100m^2) per station in the Four Seasons Bank (Weddell Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4). *S*: shallow; *M*: middle; *D*:deep.

Taxa	Stations				
	111-1	**24IIA-S**	**24IIA-M**	**24IIA-D**	**24II-B**
PAEsp2	0,0	0,0	0,0	1,7	0,0
SYN	1,8	1,2	0,5	0,6	0,0
SYNsp30	0,0	0,0	0,0	0,0	4,3
SYK	0,0	8,5	3,9	1,1	0,0
ASG	0,0	0,0	0,5	0,6	0,0
AST	3,8	11,3	7,3	25,5	5,4
ASTsp25	0,0	0,4	0,0	0,6	0,0
ACO	0,0	0,0	0,0	0,6	7,6
CUE	0,0	0,0	0,0	0,6	0,0
HEN	5,3	0,4	1,0	5,0	3,2
MAC	5,3	1,2	1,5	0,6	1,8
ODO	18,5	10,9	1,5	0,0	0,0
POR	0,9	0,4	0,0	0,0	0,5
OPH	174,0	35,5	88,0	184,9	243,8
ASA	0,0	0,0	1,5	12,2	0,0
OGI	2,6	1,6	1,0	0,0	0,0
CTE	0,0	0,0	0,0	0,0	1,8
STE	488,6	2943,1	101,2	26,6	34,5
HOL	0,0	0,0	0,0	0,0	1,8
DEN	12,3	184,5	25,9	12,2	1,8
EKM	1,2	17,8	21,5	2,2	3,2
PSO	0,9	0,4	0,0	0,0	0,0
CRI	0,9	0,8	23,5	33,3	2,2
BRY	0,9	0,0	1,3	1,8	1,8
BOD	1,8	0,0	0,5	0,6	0,0
CEL	0,0	0,0	0,0	1,4	0,0
CLN	0,0	0,0	0,5	0,6	0,5
FAS	0,0	0,0	0,5	0,0	0,0
MEO	0,0	0,0	0,0	0,6	0,0
RET	0,0	0,0	0,0	0,6	0,0
BSH	3,5	0,0	1,9	1,8	0,0
PISsp3	0,0	0,0	0,0	0,0	14,3
TRE	3,5	1,6	1,5	1,1	8,9

Table 3 Abundance of taxa (n/100m^2) per station in the Atka Bay (Weddell Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4).

Taxa	059-1	281	32II	32IV
RRC	51,8	3,0	33,4	55,0
RSY	503,9	4,0	34,8	42,1
ROF	0,0	0,0	9,5	0,0
RRbt	1,0	0,0	3,3	31,7
DEM	44,1	27,0	32,5	86,3
DEMsp12	2,1	0,0	0,0	0,0
CIA	12,3	1,5	5,7	53,4
CIB	5,6	0,0	3,5	56,5
HAL	2,1	2,0	3,3	7,9
HALsp1	3,1	0,0	0,0	0,0
HALsp2	2,1	0,0	0,0	0,0
HALsp7	1,0	0,0	0,0	0,0
HNAsp1	0,0	0,0	0,0	0,5
HOM	0,0	0,5	0,0	0,0
IOP	9,2	0,0	51,9	11,4
ISO	4,1	0,5	0,0	0,0
ISOsp2	12,8	0,5	2,9	5,5
ISOsp3	0,0	1,5	0,0	0,0
LAP	0,5	0,5	0,0	0,0
LATsp1	3,1	0,0	0,0	0,0
MOL	1,0	13,5	69,2	24,4
MYC	1,0	0,5	0,0	0,5
PII	0,5	14,5	1,0	2,0
PIN	1,0	5,5	0,0	0,5
POC	0,0	0,5	0,0	0,0
SBL	0,5	0,0	2,4	0,0
SBR	0,5	5,5	28,1	2,0
TED	7,2	8,0	9,5	4,5
TEO	1,5	0,0	0,5	0,0
TEL	15,9	2,5	1,5	25,3
TEV	1,0	0,0	0,0	0,0
YEB	171,2	0,0	78,6	34,3
FSH	0,5	133,4	0,5	3,0
HYD	380,8	265,8	139,2	138,3
HYDsp1	4,1	0,0	0,0	0,0
HYDsp2	6,2	0,5	0,0	0,0
COP	55,9	1,0	0,5	121,5
COR	1,5	0,5	0,0	0,0
OSA	0,0	175,4	3,3	0,5
SYM	19,0	0,0	0,0	0,0
LUC	1,0	1,5	0,0	0,0
ANT	0,5	0,0	1,0	9,9
ALY	0,0	0,0	0,0	2,0
GER	0,0	1,0	0,0	0,0
GOR	3,1	1,5	0,0	0,0
AIN	0,0	0,0	4,0	1,5
API	1,0	15,5	0,0	0,0

Table 3 [continued] Abundance of taxa (n/100m^2) per station in the Atka Bay (Weddell Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4).

Taxa	059-1	281	32II	32IV
ARN	0,0	3,5	0,0	0,0
DAS	2,1	6,0	3,3	1,0
PREsp1	0,5	5,0	0,0	0,5
PREsp2	0,5	5,0	0,0	0,0
PRI	17,9	8,5	21,9	5,9
THO	45,1	95,4	5,7	19,3
FAN	13,8	56,5	0,0	0,0
ACT	5,1	3,0	2,4	2,5
ACTsp6	0,0	0,0	0,0	5,9
ACTsp8	0,0	0,0	0,0	2,5
EDW	0,0	0,0	1,0	5,9
HOR	4,1	0,5	0,5	0,5
CER	8,7	1,0	0,0	0,0
NEM	0,5	0,5	0,0	0,0
NUM	3,6	0,5	1,0	0,0
NUD	1,5	1,0	0,5	0,0
RIS	0,5	0,0	0,0	0,0
PTA	0,5	0,0	2,0	1,5
SAB	10,8	0,0	4,8	5,5
SABsp3	0,0	1,0	0,0	0,0
SABsp4	5,1	23,5	1,0	0,0
SABsp5	14,9	147,4	2,9	0,0
SABsp7	192,7	0,0	0,0	0,0
SABsp11	0,0	0,5	0,5	0,0
SABsp12	1,0	23,0	0,0	0,0
POS	1,0	0,0	0,0	0,0
POSsp1	1,5	1,5	1,4	0,0
PYC	4,1	1,5	0,5	1,0
HEMsp2	0,0	0,0	1,4	0,0
HEMsp3	2,6	0,0	5,0	5,9
ASC	6,2	1,0	0,0	0,0
MOP	6,2	3,0	0,0	2,5
CIO	0,0	1,0	0,0	0,0
COL	6,2	0,0	0,0	0,5
CNV	10,3	1,0	0,0	0,5
PYU	0,5	0,0	0,0	0,0
PYB	4,1	1,0	0,5	1,0
PYD	4,6	0,5	0,0	0,5
PYS	7,7	0,5	0,0	6,4
PCL	89,2	0,0	0,0	0,0
SYA	35,4	6,0	417,7	469,9
SCY	4,1	0,0	1,0	0,5
DIS	2,1	0,0	0,0	0,0
APLsp2	1,5	0,0	23,4	4,5
APLsp3	16,4	3,0	11,4	136,3
PAEsp2	15,9	343,3	6,2	2,0
TON	0,0	0,0	18,1	3,5

Table 3 [continued] Abundance of taxa (n/100m^2) per station in the Atka Bay (Weddell Sea). For description of taxa names see list of taxa ["Labels"] (appendices 8. 4).

Taxa	059-1	281	32II	32IV
SYN	7,7	7,9	1,0	0,0
SYNsp31	0,0	7,0	0,0	0,0
SYK	6,2	16,0	17,6	18,8
AST	20,0	11,5	5,2	5,5
ACO	0,5	0,0	2,9	1,0
CUE	1,5	0,0	0,0	0,5
HEN	5,1	4,0	1,0	4,0
MAC	1,0	0,5	0,5	3,5
ODO	1,0	0,0	0,0	0,0
POR	0,0	0,5	0,0	0,0
OPH	593,6	92,4	291,7	136,8
ASA	2,6	0,0	0,0	0,5
OGI	0,5	1,5	1,0	0,5
CID	17,9	0,0	2,9	5,0
CTE	0,0	0,0	12,4	6,4
OTO	0,0	0,0	2,9	12,9
STE	26,1	1,0	0,5	0,0
IRR	0,0	0,0	6,7	2,0
HOL	3,1	0,0	0,0	0,0
DEN	217,8	38,5	27,6	5,7
EKM	94,8	38,5	8,7	8,9
PSO	2,6	0,0	1,0	1,0
TAE	3,6	0,0	1,0	0,5
CRI	54,3	39,5	86,3	37,7
BRY	3,1	0,5	0,0	2,5
BRYsp7	0,0	1,0	0,0	0,0
ALC	0,5	26,0	0,0	3,5
AUS	8,2	0,0	0,0	0,0
BOD	16,9	13,0	12,9	3,5
CAR	0,5	0,5	0,0	0,0
CAT	2,1	0,0	1,0	0,5
CEL	20,0	19,5	3,3	3,5
CHO	11,8	2,5	2,4	16,4
CLN	6,2	6,5	17,6	9,9
CYCsp1	0,5	3,0	9,5	0,0
FAS	6,2	2,0	0,0	0,0
FLU	0,0	0,5	0,5	0,5
KYM	9,7	1,0	0,0	0,0
LAG	14,4	0,0	7,1	15,9
MEO	488,5	236,8	3863,8	274,1
RET	0,5	0,5	0,0	0,5
BSH	4,1	6,0	0,0	0,5
CHI	0,0	1,0	0,0	0,0
PAG	0,0	0,0	0,5	0,0
TRE	9,2	0,0	1,4	5,0

8.4 List of taxa

Here I present the list of the mega-epibenthic taxa identified and analysed at shallow-water stations in the Bellingshausen and Weddell seas, Antarctica.

Porifera	"LABELS"
Class Hexactinellida	
Rosella fibulata	ROF
Rosella racovitzae	RRC
Rosella racovitzae (budding type)	RRb.t.
Scolymastra joubini / Rosella nuda	RSY
Class Demospongiae	
Calyx spp.	CAL
Cinachyra antarctica	CIA
Cinachyra barbata	CIB
Clathria nidificata	CTN
Clathria pauper	CTH
Demospongiae spp.*	DEM
Demospongiae sp.12	DEM sp12
Demospongiae sp.13	DEM sp13
"Fan shape"	FSH
Guitarra fimbriata	GUI
Haliclona sp.	HNA
Haliclona sp.1	HNA sp1
Haliclonidae spp.	HAL
Haliclonidae sp.1	HAL sp1
Haliclonidae sp.2	HAL sp2
Haliclonidae sp.3	HAL sp3
Haliclonidae sp.7	HAL sp7
Haliclonidae sp.8	HAL sp8
Haliclonidae sp.9	HAL sp9
Haliclonidae sp.10	HAL sp10
Haliclonidae sp.11	HAL sp11
Homaxinella spp.	HOM
Inflatella belli	INF
Iophon radiatus	IOP
Isodictya spp.	ISO
Isodictya sp.1.	ISO sp1
Isodictya sp.2.	ISO sp2
Isodictya sp.3.	ISO sp3
Latrunculia sp.1	LAT sp1
Latrunculia apicalis	LAP
Latrunculia brevis	LAV
Latrunculia spp.	LAT
Monosyringa longispina	MOL
Mycale acerata	MYC
Phorbas areolata	PHO
Poecilosclerida spp.	POC
Polymastia invaginata	PIN
Polymastia isidis	PII
Stylocordyla borealis (oblong)	SBL
Stylocordyla borealis (round)	SBR
Tedania oxeata	TEO
Tedania tantula	TED
Tedania vanhoeffeni	TEV
Tentorium semisuberites	TEN
Tetilla leptoderma	TEL
"Yellow branches"	YEB

Cnidaria

Class Hydrozoa

Corymorpha parvula	COP
Corymorpha spp.	COR
Corymorpha sp.1	COM
Hydrodendron arborea	DRO
Hydrozoa sp.1	HYD sp1
Hydrozoa sp.2	HYD sp2
Hydrozoa sp.3	HYD sp3
Hydrozoa sp.4	HYD sp4
Hydrozoa sp.5	HYD sp5
Hydrozoa sp.6	HYD sp6
Hydrozoa sp.7	HYD sp7
Hydrozoa sp.8	HYD sp8
Hydrozoa spp.*	HYD
Oswaldella antarctica	OSA
Schizotricha cf. *unifurcata*	SCH
Schizotricha sp.2	SCH sp2
Symplectoscyphus spp.	SYM
Tubularia ralphii	TUB

Class Scyphozoa

Lucernaria spp.	LUC

Class Anthozoa

Anthozoa spp.*	ANT

Subclass Octocorallia

Clavularia cf. *frankliniana*	CLA

Alcyonacea

Alcyonacea spp.*	ALY
Alcyonacea sp.5	ALY sp5
Alcyonium spp.	ALM
Gersemia spp.	GER

Pennatulacea

Umbellula spp.	UMB

Gorgonacea

Ainigmaptilon antarcticum	AIN
Arntzia sp.	ARN
Ascolepis spinosa	API
Dasystenella spp.	DAS
Fannyella spp.	FAN
Gorgonacea sp.11	GOR sp11
Gorgonacea spp.*	GOR
Isididae spp.	IDI
Notisis spp. / *Tenuisis* spp.	ISI
Primnoella sp.1.	PRE sp1
Primnoella sp.2.	PRE sp2
Primnoisis spp.	PRI
Thouarella spp.	THO
Tokoprimno spp.	TOK

Subclass Hexacorallia

Actiniaria

Actinaria sp.3	ACT sp3
Actinaria sp.6	ACT sp6
Actinaria sp.8	ACT sp8
Actinaria sp.9	ACT sp9

Actinaria sp.13	ACT sp13
Actinaria sp.16	ACT sp16
Actinaria sp.18	ACT sp18
Actinaria sp.19	ACT sp19
Actinaria sp.20	ACT sp20
Actinaria spp.*	ACT
Capnea georgiana	CAP
Corallimorphus profundus	COF
Edwardsia spp.	EDW
Hormathia spp.	HOR
Isosicyonis alba	ICY
Urticinopsis antarcticus	URT
Ceriantharia	
Ceriantharia spp.*	CER
Ceriantharia sp.2	CER sp2
Ceriantharia sp.5	CER sp5

Bryozoa

Class Stenolaemata

Alcyonidium spp.	ALC
Austroflustra spp.	AUS
Bostrychopora dentata	BOD
Bryozoa sp.7	BRY sp7
Bryozoa sp.19	BRY sp19
Bryozoa spp.*	BRY
“Bush complex”*	BSH
Camptoplites tricornis	CAT
Carbasea curva	CAR
Cellaria spp.	CEL
Cellarinella spp.	CLN
Chondriovelum adeliense	CHO
Cyclostoma sp.1	CYC sp1
Fasciculipora spp.	FAS
Flustridae sp.2	FLU sp2
Flustridae spp.	FLU
Kymella polaris	KYM
Lageneschara spp.	LAG
Melicerita obliqua	MEO
Nematoflustra spp	NEF
Orthoporidra compacta	ORT
Reteporella spp.	RET

Nemertini

Nemertini spp.*	NEM

Echiura

Echiura sp.2	ECH sp2

Mollusca

Austrodoris kerguelensis	RIS
Buccinulidae spp.	BUC
Harpovoluta charcoti	HAR
Marseniopsis mollis	MAR
Neobuccinum eatoni	NEO
Nudibranchia spp.	NUD
Nuttallochiton mirandus	NUM

Annelida	
Class Polychaeta	
Errantia	
Flabelligeridae spp.	FLA
Sedentaria	
Pista spp.	PTA
Sabellidae sp.1	SAB sp1
Sabellidae sp.3	SAB sp3
Sabellidae sp.4	SAB sp4
Sabellidae sp.5	SAB sp5
Sabellidae sp.7	SAB sp7
Sabellidae sp.9	SAB sp9
Sabellidae sp.11	SAB sp11
Sabellidae sp.12	SAB sp12
Sabellidae spp*.	SAB
Polychaeta sedentaria spp.	POS
Polychaeta sedentaria sp.1	POS sp1
Polychaeta sedentaria sp.2	POS sp2
Telepus-Typ	PUS
Pycnogonida	
Pycnogonida spp.*	PYC
Colossendeis spp.	EIS
Crustacea	
Isopoda	
Glyptonotus antarcticus	GLY
Hemichordata	
Class Pterobranchia	
Pterobranchia sp.2	HEM sp2
Pterobranchia sp.3	HEM sp3
Echinodermata	
Class Asteroidea	
Acodontaster spp.	ACO
Asteroidea spp.*	AST
Asteroidea sp.3	AST sp3
Asteroidea sp.25	AST sp25
Cuenotaster involutus	CUE
Diplasterias brucei	DIP
Henricia spp.	HEN
Labidiaster anulatus.	LAB
Leptychaster spp.	LEP
Lophaster tenuis	LOP
Macroptyaster spp.	MAC
Odontaster validus	ODO
Perknaster aurorae	PEK
Porania spp.	POR
Remaster gourdoni	REM
Solaster regularis subarcuatus	SOR
Class Ophiuroidea	
Astrotoma agassizii	ASA
Ophiosparte gigas	OGI
Ophiuroglypha carinifera	OCA
Ophiuroidea spp.*	OPH

Class Echinoidea	
Cidaridae spp.	CID
Ctenocidaris spp	CTE
Irregularia spp.	IRR
Notocidaris spp	OTO
Sterechinus neumayeri	STE
Class Holothuroidea	
Bathyplotes fuscivinículum	BAF
Bathyplotes spp.	BAT
Dendrochirotida sp.2	DEN sp2
Dendrochirotida spp.*	DEN
Ekmocucumis turqueti	EKM
Holothuroidea sp.10	HOL sp10
Holothuroidea sp.11	HOL sp11
Holothuroidea spp.*	HOL
Psolus spp.	PSO
Taeniogyrus contortus	TAE
Class Crinoidea	
Crinoidea spp.*	CRI
Chordata	
Class Ascidiacea	
Aplidium sp.1	APL sp1
Aplidium sp.2	APL sp2
Aplidium sp.3	APL sp3
Aplidium sp.5	APL sp5
Ascidiacea sp.17	ASC sp17
Ascidiacea spp.*	ASC
Corella eumyota	COL
Ciona antarctica	CIO
Cnemidocarpa verrucosa	CNV
Distaplia spp.	DIS
Molgula pedunculata	MOP
Pyura bouvetensis	PYB
Pyura discoveryi	PYD
Pyura setosa	PYS
Pyura spp.	PYU
Scycozoa sp.1	SCY
Synascidiacea sp.30	SYN sp30
Synascidiacea sp.31	SYN sp31
Synascidiacea spp.*	SYN
Synoicum adareanum	SYA
Polycitoridae sp.2	PAE sp2
Polyclinidae spp.	PCL
Polyclinidae f2	PCL f2
Polysyncraton trivolutum	TON
Synascidiacea sp.32	SYN sp32
Pisces*	
Chinodraco myersi	CHI
Cygnodraco mawsoni	CYG
Muraenolepis spp.	MUR
Pagetopsis macropterus	PAG
Pisces sp.1	PIS sp1
Pisces sp.2	PIS sp2
Pisces spp.	PIS
Trematomus spp.	TRE

* taxa excluded from diversity analysis